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Temporal changes in food resource availability between two karst bat assemblages

by

Tlaishego Tedson Nkoana

17380023

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Supervisor: M Keith

Co-supervisor: ECJ Seamark

Disclaimer

This is not a traditional Master's dissertation with an outline of a single introduction, methods, results and discussion sections. Instead, the format of this dissertation has two research chapters each having an introduction, methods, results, discussion and conclusion sections. The intention behind the said format is to submit each research chapter to scientific journals for publishing. There is also repetition within the thesis due to cross referencing of results between chapters.

Declaration

I, Tlaishego T Nkoana declare that the work presented in this thesis, which I hereby submit for the degree Master of Science at the University of Pretoria, is my own work and has never been submitted for any degree or examination at any other tertiary institution, and that all the sources I have used or quoted have been acknowledged by complete reference.

Tlaishego T Nkoana

Signature___________________

Date_______________________

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Summary

The temporal availability of arthropods varies in response to changing quality of vegetation which is influenced by climatic conditions. Climate in the Savanna and Grassland biomes is defined by wet and dry cycles. Bats (Chiroptera) are major consumers of nocturnal flying arthropods and respond to temporal fluctuations of their arthropod prey as well as climatic conditions. My study is undertaken in two karst landscapes within two biomes, Savanna (Meletse) and Grassland (Cradle of Humankind World Heritage Site-CoH WHS). The migratory *Miniopterus natalensis* utilizes Madimatle cave (Meletse –Thabazimbi) for maternity roosting (October-February/March) whilst caves in the CoH WHS provide hibernacula (winter) roosts (April-September) for this population.

Migration in bats has been linked to changing climatic conditions for temperate species and food availability in tropical species. The factors driving the migration of *Min. natalensis* population are not yet understood. The temporal changes of bat assemblages and their arthropod prey from dry to wet season climatic regimes are of interest. To test this, I collected arthropods and recorded bat echolocation calls from dry to wet season (June-February), using malaise traps and Anabat SD2 bat detectors, respectively. Different bat species are adapted to forage within different levels of vegetation clutter. Traps and bat detectors were therefore spatially placed across different levels of vegetation clutter at the study sites. Arthropods were caught, measured (size and biomass) and capture success (CS=individuals/trap-hours) were calculated monthly. An Acoustic Activity Index (AAI) of recorded bats was also used to obtain monthly relative activity.

My results show that bat activity corresponds to arthropod availability on a temporal basis with wet season highs and dry season lows, at both study sites. When comparing Grassland and Savanna sites, arthropod CS was significantly higher ($P<0.01$) at the grassland (mean CS=0.248 ind./trap) whilst biomass was greater at the savanna site. In addition, the Grassland had higher CS with lower biomass for the arthropods Diptera and Lepidoptera, whilst the larger biomass taxa, Coleoptera and Hemiptera, had higher CS at the savanna. The frequency of larger arthropods was higher in November and corresponded with peak biomass measured that month. At Meletse, significant increases ($P<0.05$) for bat activity and arthropod CS were recorded in August/September (late dry season) and November (wet season). Species level bat activity increases corresponded with increases in arthropod CS and biomass.

The matching between bat activity patterns and arthropod availability is important for the maternity season when pregnant females have to meet increased energy demands. Indeed, the maternity season matched with periods of highest food resources expressed as increased arthropod abundance and biomass. Greater bat activity during the maternity period places Meletse as an important food resource reservoir both supporting resident and the migratory species.

As bats are major predators of several taxa of nocturnal flying arthropods amongst which are agricultural pests, the ecological and economic implications of maintaining healthy bat assemblages remain of importance. Careful and effective monitoring of bat assemblages and arthropod prey will further increase understanding of the temporal dynamics between predator activity and prey abundance within habitats. Knowledge on the effects of land-use change on habitats will develop a better understanding of impacts on species and broader ecological systems.

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Chapter 1: General Introduction

Arthropods are considered the most successful animal group in terms of geographic spread, variation and overall contribution to ecosystems in which they occur (Evans & Wigglesworth 1988; Sanchez-Bayo & Wyckhuys, 2019). Collectively, arthropods have a greater number of species than other animal group and this is reiterated by the approximately 1.2 million extant species of insects within the Arthropoda phylum (Zhang, 2011). Temporally, the abundance of arthropods varies, and this influences their function, amongst others, to serve as a food source within ecosystems (Costanza *et al*., 1997). Assemblages of herbivorous arthropods rely on the temporal availability of plants as a food source to survive (Barnett & Facey, 2016). The quality and abundance of vegetation responds directly to temporal changes in climatic conditions therefore the temporal abundance of arthropods is influenced by prevailing combinations of precipitation and temperature (Barnett & Facey, 2016; Berridge, 2012; Pinheiro *et al*., 2002; Schowalter, 2011).

Under the influence of temporally changing climatic regimes, changes in arthropod abundance and richness therefore has a cascading effect on the predator species, at higher trophic levels, that rely on arthropods as a food source (Hagar *et al*., 2012; Verrastro & Ely, 2015). It is therefore not surprising that the activity patterns of arthropod predators are associated with their prey (Churchill, 1994; Hagar *et al*., 2012; Omogbeme & Oke, 2018; Dinaw *et al*., 2017, Verrastro & Ely, 2015; Wang *et al*., 2010). Arthropods are therefore an important contributor of energy within ecosystems through food resource acquisition by predator species (Crossley & Howden, 1961). A major predator of arthropods are bats (Order Chiroptera) which consist of some 1300 species and 70% of which forage on nocturnal flying arthropods, primarily insects (Jones *et al*., 2009; Monadjem *et al*., 2010; Teeling *et al*., 2018). For example, an estimated 1000 tons of insects are consumed nightly by the several *Tadarida brasiliensis* occupying the Bracken Cave and surrounding major caves in Texas (McCracken, 1996; Monadjem *et al*., 2010).

As arthropod foragers, bats have been identified as having an economic benefit in agriculture (Cleveland *et al*., 2006). This is attributed to bats high consumption of nocturnal flying arthropods and agricultural pests forming part of their diet (Aizpurua *et al*., 2018; Boyles *et al*., 2011; Cleveland *et al*., 2006; Kunz *et al*., 2011). The Lepidoptera and Scarabaeidae taxa, for example, make up a significant part of the diet of several insectivorous bats (Findley & Black, 1983) with some important pest species found within these groups (Scholtz & Holm, 1985). Examples include *Busseola fusca* (stalk borer), *Spodoptera exempta* (army worms) and Spodoptera littoralis (cut worms) of the Lepidoptera as well as leaf chafers and rhinoceros beetle larvae of the Scarabaeidae (Scholtz & Holm, 1985). Bats are therefore in a good position to act as a biological control to suppress arthropod pest populations. Taylor *et al*. (2017) reported on heightened bat activity coinciding with temporal peaks in the abundance of arthropods particularly those of the known pests *Cryptophlebia ombrodelta* (Macadamia Nut Borer Moth), Nezara sp. (Green Stinkbugs), and *Bathycoelia natalicola* (Twin-Spotted Stinkbugs) within the fruit growing area of the Levhuvhu Valley, Limpopo Province, South Africa. Furthermore, a study undertaken in the midwestern United States of America (USA) reported that *Acalymma vittatum* (Cucumber beetle) larvae feed on the roots of corn which lowers productivity by 10-13%. Based on calculations, it was estimated that *Eptesicus fuscus* (Big Brown Bat) can inhibit the production of 33 million *Aca. vittatum* eggs by annually consuming about 600,000 adult beetles in the USA (Whitaker, 1995). Cleveland *et al*. (2006) showed that *Tad. brasiliensis* (Brazilian Free-tailed Bat) protected crops from damage and reduced the use of pesticides in Texas (USA), thus providing both economic and environmental benefits. Understanding the activity patterns of bats and their food sources is therefore important in order to help maximise their ecological and economical role.

These ecological and economic roles are compromised by impacts of human disturbance which can potentially alter the functioning of ecological processes and therefore compromise ecosystems (Naeem *et al*., 1999). These ecological processes drive environmental conditions under the influence of the diversity of plants, animals and microbial species (Naeem *et al*., 1999). Human disturbances can be in the form of land-use change which has been associated with biodiversity loss (Birkhofer *et al*., 2015). Species groups such as arthropods are affected by impacts of land–use change such as intensive habitat fragmentation, urbanisation and agriculture through the stimulation or reduction of available niche-space (Birkhofer *et al*., 2015; Sanchez-Bayo & Wyckhuys, 2019). As such, changes in land–use either reflect positively or negatively on the abundance and variation of arthropods (Birkhofer *et al*., 2015; Schowalter, 2011). As arthropods are a food source to several animals (Costanza *et al*., 1997), understanding the impacts of land–use change on affected arthropod species will help better understand how predator species are affected by land–use change through trophic cascades.

Of interest to the present study is arthropod availability (food resource) as well as bat assemblages (predator) located in two separate karst landscape systems in South Africa (SA) which are Savanna and Grassland based (Figure 1.1). Karst landscapes comprise of cave systems which provide essential habitats for cave–roosting bat species (Clement *et al*., 2006; Struebig *et al*., 2009) although other bat species roost in trees, crevices and man-made structures (Monadjem *et al*., 2010). Caves provide roosting sites to some of the largest populations of bats including, for example, the millions of bats found in Bracken Cave and other major caves in central Texas (McCracken, 1996). Large populations of bats are also found in the De Hoop Guano Cave in the Western Cape, South Africa (Monadjem *et al*., 2010), and Gladysvale (Gauteng Province) and Meletse (Limpopo Province) caves in South Africa (van der Merwe, 1973b, 1975).

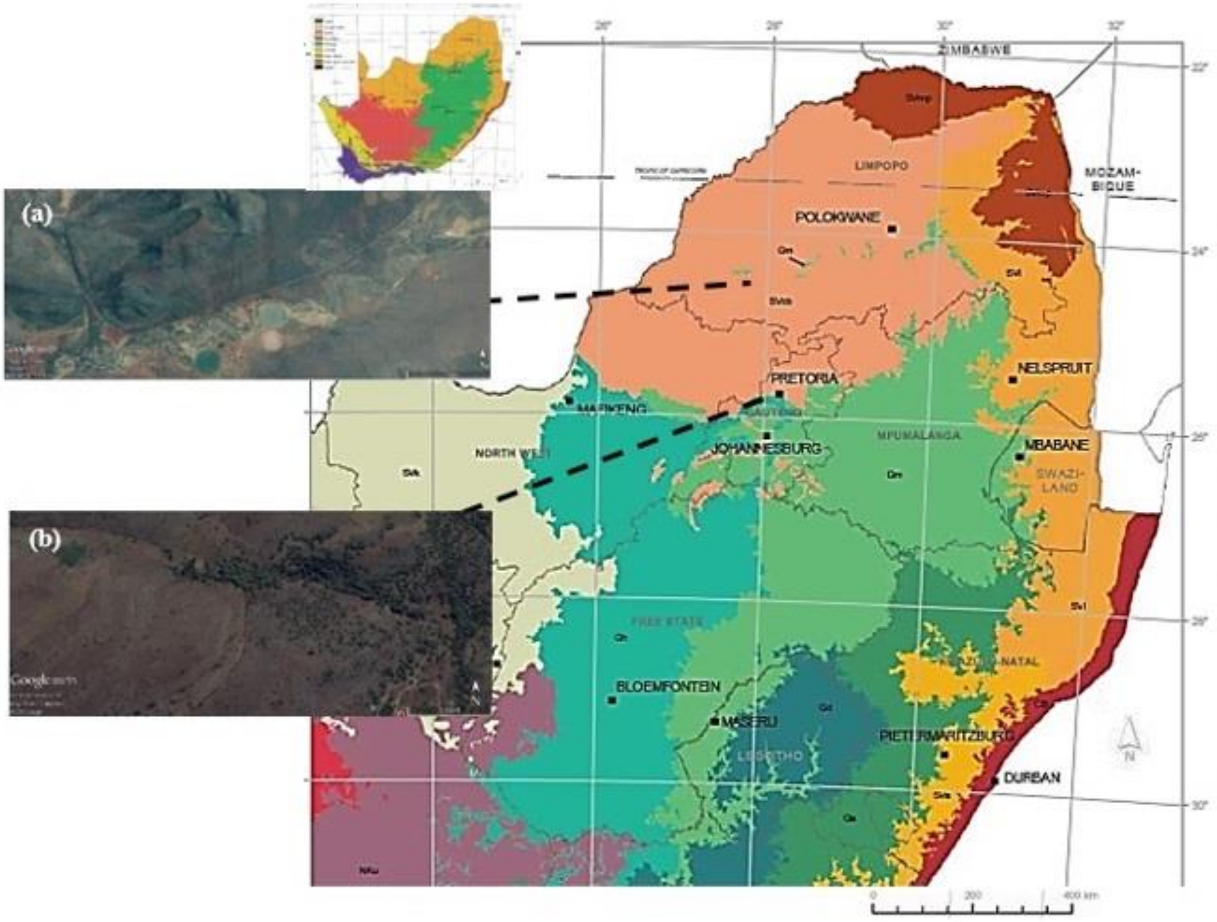

Figure 1.1: The location of the karst landscape systems of (a) Meletse in Limpopo Province (Savanna biome) and (b) Cradle of Humankind World Heritage Site in Gauteng Province (Grassland biome), South Africa. Map (including insert map), Rutherford *et al*. (2006b). (a) & (b), Google Earth (Accessed 11 August 2017).

Interestingly, some of the caves found in the Savanna and Grassland karst systems (Gauteng and Limpopo provinces, South Africa, Figure 1.1) host a population of *Miniopterus natalensis* which has been recorded to migrate between the two karst systems (van de Merwe, 1973b, 1975). The migration of bat species in temperate regions such as Southern Africa (SA) is associated with the need for both hibernation and maternity roosting sites (Moussy *et al*., 2013). This in turn, is driven by climate conditions. It has been found that sites that are chosen as hibernacula sites need to offer optimal climatic conditions with stable low temperatures and enough humidity while maternity roosting sites need to have higher temperatures in order to help the bats remain active (Moussy *et al*., 2013). Findings by van de Merwe (1973b, 1975) revealed that the cave–dwelling *Min. natalensis* hibernates in the Grassland caves found around the Cradle of Humankind World Heritage Site (CoH WHS) during the autumn and winter period (April to August). Individuals of the population migrates to the Savanna caves, such as Meletse in Limpopo during spring and summer (September to February/March) for maternity roosting (van der Merwe 1975).

Several other bat species inhabit caves at both karst systems (ACR, 2018; Chege *et al*., 2015; Kearney *et al*., 2017) although it is unknown whether they also migrate or stay at respective karst systems throughout the year. Studies have shown that bat species respond to temporal increases and decreases in arthropod abundance as a food source (Churchill, 1994; Dinaw *et al*., 2017; Wang *et al*., 2010). This links back to arthropod availability which fluctuates temporally under the influence of climatic conditions (Barnett & Facey, 2016; Berridge, 2012; Pinheiro *et al*., 2002; Schowalter, 2011). Although it is evident that a variety of bat species utilize both karst landscape systems in the present study (Kearney *et al*; 2017; ACR, 2018), information on the availability of food resources which potentially support these bat assemblages is lacking.

From a biome perspective, the Savanna and Grassland biomes in SA have similar climatic regimes (Du Toit & Cumming 1999; Mucina & Rutherford, 2011). Both biomes have distinctly different seasons which are characterised by temporal fluctuations in temperature and precipitation to make two contrasting seasons: the dry (cooler temperature and lower precipitation) and wet (warmer temperature and higher precipitation) seasons (Rutherford *et al*., 2006b; Schowalter, 2011). Botha *et al*. (2016) hypothesised that the structural complexity of the Savanna biome of SA (i.e the presence of trees and shrub layers) enables greater abundances per unit area and variation of arthropod species as compared with less complex structures of the Grassland biome. Botha *et al*.

(2016) tested this hypothesis but were unable to prove it, instead their results seemed to indicate that geographical position (longitude and latitude) better explains arthropod assemblages than biome characteristics. They suggest that arthropod variety and abundance could be more effected by altitude as localities generally increase in altitude from north to south, and climate as localities become drier from east to west.

Study aim

Findings by Botha *et al*. (2016) and other studies (Adams *et al*., 1981; Eyre *et al*., 2001; Gutiérrez & Menéndez, 1995) have reported on the influence of altitude on the species composition of several arthropod groups. Interestingly, van de Merwe (1973b) reported the grassland based CoH WHS caves at 1280m and the savanna based Meletse caves at 1115m. Furthermore, the study by Botha *et al*. (2016) under-represented the temporal influence of climatic conditions on arthropod taxa abundance (Barnett & Facey, 2016; Berridge, 2012; Pinheiro *et al*., 2002; Schowalter, 2011). I aim to make a comparison between dry and wet season arthropod availability and abundance between the Savanna and Grassland biomes by collecting arthropods at the areas around the Meletse cave, Limpopo (Savanna) and at the CoH WHS, Gauteng Province (Grassland) (Figure 1.1). Furthermore, I investigate the availability of food resource and bat species activity found at both biomes (ACR, 2018; Kearney *et al*., 2017) from the dry to wet season. I hypothesise that arthropod availability and abundance will coincide with the activity of bats at each biome. In addition, the role of food resource availability as a potential driver of *Min. natalensis* migration between the mentioned Savanna and Grassland karst systems will be better understood.

Outline

Following this brief general introduction (**Chapter 1**) this thesis is written as two research chapters (**Chapter 2 and 3**). **Chapter 2** focuses on temporal changes in arthropod availability in two karst landscapes of the Savanna and Grassland biomes. The count and biomass of collected arthropods was used as a proxy for food resource availability. Arthropod availability was investigated and compared between the months of June 2017 to February 2018 (spanning the dry to wet season) as well as within different patches of vegetation clutter (density of vegetation within a plot) at the Savanna. Arthropod availability from September to January (late dry to mid–wet season) was also compared between the Grassland and Savanna. **Chapter 3** focuses on bat activity and food resource availability within karst landscapes of a Savanna and Grassland biome. Sampling of bat activity was undertaken concurrently with that of **Chapter 2**’s arthropod sampling, using bat acoustic data as a proxy for relative activity. Also, in **Chapter 3**, I further compared bat activity at the Savanna site across the different months and within different patches of vegetation clutter for the Savanna and related this to food resource availability. Furthermore, a comparison was made between Grassland and Savanna arthropod availability and bat activity between September and January (late dry to mid–wet season). This thesis also has a general conclusion and recommendations for future work (**Chapter 4**).

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Chapter 2: Temporal changes in food resource availability: Arthropod abundance and biomass in Savanna and Grassland areas, northern South Africa

2.1: Introduction

Arthropods form the main or partial food resource of several vertebrate species (Hagar *et al*., 2012; Verrastro & Ely, 2015). For example, the diet of *Catharus ustulatus* (Swanson's thrush) primarily consists of arthropods and few fruits (Hagar *et al*., 2012). Furthermore, Verrastro & Ely (2015) reported that the diet of *Liolaemus occipitalis* (lizard) primarily consists of Coleoptera and Hymenoptera arthropods. The mammalian order Insectivora was historically recognized on the basis of feeding on arthropods (primarily insects) and consisted of approximately 450 species (Gunnel & Bloch, 2008; Wilson & Reeder, 2005). Another mammalian taxon, the Chiroptera, are recognized as major predators of arthropods (particularly nocturnal flying insects) with approximately 70% of the bat species preying on arthropods whilst the rest are frugivorous and a few others are carnivorous (Monadjem *et al*., 2010). For semantic purposes, the term 'arthropod(s)' is used in place of 'insect(s)' throughout unless referring exclusively to insects. This is due to non-insect arthropod families forming part of sample captures despite insects forming the constituency. Predators are influenced by the spatial and temporal availability of food resources which is determined by the distribution and abundance of prey species (Schowalter, 2011). Here, a distinction is made between availability (presence and quantifiable measure within the habitat) and abundance (count of individual arthropods) of athropods as these are reflected differently in the diet of predator species.

The temporal availability and abundance of arthropods is influenced by variations in climatic and vegetation regimes (Barnett & Facey, 2016; Barton *et al*, 2009; Pinheiro *et al*., 2002; Schowalter, 2011). Arthropod predators in temperate environments are confronted with fluctuations in food availability and cope by applying a variety of strategies including migration, utilizing alternative food sources or entering torpor (Morse, 1971). Nonetheless, their phenology is comprised of low and high energy demanding periods. Studies on small insectivorous mammals have shown an alignment between temporal activity patterns of predator species and their prey whereby breeding coincides with heightened food resource availability (Churchill, 1994; Omogbeme & Oke, 2018;

Dinaw *et al*., 2017, Wang *et al*., 2010). The availability of food resources within areas found in the largest biomes in South Africa, the Savanna and Grassland (Rutherford *et al*., 2006b), is explored in this study. These biomes are defined along their respective arrangement of vegetation structures (Rutherford *et al*., 2006b).

Botha *et al*. (2016) reported on the potential of using arthropods for studies comparing species diversity and abundance between biomes. Such comparison is especially apparent when the arthropod populations comprise phytophagous and host-specific species (Moolman *et al*., 2013). The Savanna biome consists of herbaceous layer dominated by various grass species (bottom layer) and patches of woody component composed of shrubs and trees (middle and top layers). The woody component forms an irregular series of interlocking canopies and openings and serves an important function for animals. For example, tree height and dense woody entanglements determines available shade and provides protection against predators (Rutherford *et al*., 2006a). The dense vegetation clutter of the woody component affects the amount of rainfall that reaches the soil (Rutherford *et al*., 2006a). During periods of extended rainfall, savanna deciduous woody species usually retain their leaves for longer periods (Rutherford *et al*., 2006a) resulting in extended dense clutter well into the next flush of leaves. Fire also drives the density of clutter in the savanna as it maintains tree and shrubs to acceptable heights for browsers. The effects of fire varies for different trees based on their heights. Jordaan (1995), for instance, showed that in a burnt area of the Central Bushveld dominated by *Dichrostachys cinerea* (Sicklebush) and *Vachellia gerrardii* (Red thorn), trees of less than 3m tall were greatly reduced in height whilst the top layer of trees 3m and higher were unaffected.

Grasslands are structurally less complex and dominated by members of the grass group Poaceae (Mucina & Rutherford, 2011). Expectedly, the vertical layer is predominantly defined by the height of the dominating grass. Strong interactions between precipitation patterns (availability of moisture), grazing pressure, the occurrence of fire, and soil type (nutrient availability) determine grassland vegetation structure (Mucina *et al*., 2006). The subfamilies Panicoideae, Arundinoideae, Chloridoideae and Pooideae are amongst the grass groups occurring in the Grassland biome with Panicoideae having higher species diversity than others (Mucina *et al*., 2006). Changes in precipitation patterns lead to temporal variations in plant composition and primary production in grasslands (Barnett & Facey, 2016). Annual precipitation and temperature peaks in grassland coincide with peak plant production. In contrast, periods of low precipitation and temperature coincide with near complete termination of vegetation activity (Mucina *et al*., 2006). Fire maintains the structure of a grassland by limiting succession of shrubland-to-forest in areas receiving more than 650mm annual rainfall. In the absence of fire, areas with lower annual rainfall (less than 650mm) are more prone to increase in tree density associated with no changes in the composition species (Mucina *et al*., 2006). The frequency, seasonality and intensity of fires are key factors in their influence on the landscape (Mucina *et al*., 2006). Lightning strikes are the natural ignition of fires in grasslands. Therefore, the occurrence of natural fires in grasslands maintains the dominance of grass species over woody species in a Grassland landscape (Mucina *et al*., 2006).

Barnett & Facey (2016) reported that seasonal changes in precipitation have direct and indirect impacts to affected arthropod species in Grasslands. Direct impacts are observed when individuals show behavioral or physiological responses as a direct consequence of changes in water availability (Barnett & Facey, 2016). During the dry season, most aboveground arthropods evade dehydration by migrating or entering a quiescent state in the soil. Morphological characteristics can limit or promote survival during dry periods, for instance, soft-bodied arthropods are more vulnerable in dry conditions due to lacking a waxy cuticle which reduces evaporation of water (Berridge, 2012). The wet season brings about a challenge of coping with excess moisture to many arthropods. Some arthropods are morphologically equipped to tolerate higher degrees of water than others, such as the larger species of Lepidoptera that can tolerate water much longer and better than smaller Lepidoptera (Barnett & Facey, 2016). Other arthropods employ submersion tolerance mechanisms or shelter-seeking to cope with rainfall (Barnett & Facey, 2016).

Indirect impacts occur when the food source population (usually plants) of arthropods respond to changes in water availability which thereby affects the herbivorous population (Barnett & Facey, 2016). Plant biomass, productivity and quality diminish during the dry season which may affect the survival of herbivores either negatively or positively. Walter *et al*. (2012) demonstrated that lower soluble protein content in dried *Holcus lanatus* (Yorkshire fog grass) delayed development and increased mortality rates in *Spodoptera sp.* (army worm) larvae as compared to individuals which consumed non-dried grass. The reduced plant growth resulting from low precipitation in the dry season is associated with lower abundance of herbivorous arthropod species. Meanwhile, periods of increased precipitation (wet season) stimulate plant productivity and, subsequently, results in increased abundance of herbivorous arthropods (Barnett & Facey, 2016). However, Barton *et al*., (2009) demonstrated how increased precipitation resulted in decreased survival of grasshoppers (order Orthoptera). Both increased and reduced precipitation affect different species of arthropods in various ways. Schowalter *et al*. (1999) concluded that responses to environmental changes are linked to physiological optimums of herbivorous arthropod species and responses of plant food species.

Vegetation regimes in the Savanna and Grassland biomes differ in terms of complexity of vegetation structure (Botha *et al*., 2016). Mucina *et al*. (2006) described vegetation structure as the vertical, horizontal and temporal arrangement of vegetation. Differences are described in terms of density of basal (portion of the plant which grows into the soil) and canopy (area beneath the plant that clutters soil surface) clutter. Schadek *et al*. (2008) found a robust link between vegetation structure and plant species richness whilst Botha *et al*. (2016) further associated complex vegetation structure with higher arthropod abundance. The complex vegetation structure observed in cluttered vegetation spaces (mixture of grass, shrub and trees) of the Savanna is therefore expected to have higher arthropod availability than the much simpler open vegetation structure of the Grassland.

In the context of species diversity comparison between the Savanna and Grassland biomes, the former has greater structural complexity which allows for higher inhabitation of arthropod species and abundance as compared to the simpler Grassland (Botha *et al*., 2016). Variations (intra and inter) in arthropod abundance for the Savanna and Grassland biomes are therefore expected. Botha *et al*. (2016) explored this by comparing arthropod order assemblages between Savanna and Grassland areas of South Africa as seen in Table 2.3.4. To coincide with maximum biological activity, Botha *et al*. (2016) collected arthropods in the morning during the months of January and February. However, the aspect of seasonal fluctuations was under-represented by Botha *et al*. (2016).

The evaluation of arthropod biomass has been shown to be an important aspect in ecological studies involving arthropod surveying (Rotenberry, 1980). Biomass, defined here as the dry weight of sampled organisms from an area, has been used as a proxy for production (Jenkins, 2015).

Biomass is measured as the mass quantity of organisms in space and time while production refers to the rate of generating new biomass at a place overtime (Jenkins, 2015). Despite being fundamentally different, Jenkins (2015) reported a strong relationship between insect biomass and production after performing ordinary least squares regression analysis. Towers *et al*. (1994) used biomass to calculate secondary production in aquatic stream studies. Without making direct inference to the quantity of food resource production (arthropod), biomass can be used as a proxy for food resource availability. In the context of predator-prey co-existence, expected food resource partitioning is defined along differences in prey taxa consumed, prey size and foraging microhabitats (Rotenberry, 1980).

Arthropod abundance and distribution is subject to local climatic conditions which fluctuates temporally (Barnett & Facey, 2016; Berridge, 2012; Pinheiro *et al*., 2002; Schowalter, 2011). Botha *et al*. (2016) further reported that greater vegetation complexity accommodates greater arthropod abundance. It is therefore hypothesized that temporal variations in arthropod availability, based on prevailing local climatic conditions (dry or wet), reflect in their abundance and biomass. It is further hypothesized that arthropod availability varies across patches of vegetation which exhibit different level of vegetation clutter. The objectives of this study are to therefore (1) investigate temporal changes in arthropod availability and abundance across the dry to wet season, and (2) compare differences in arthropod availability and abundance across different vegetation strata within a Savanna based area. In terms of food resource availability comparison, it is hypothesized that the Savanna has greater arthropod availability than the Grassland.

2.2: Methods

Ethics and Permits

The arthropods and bat acoustic data used in this study did not require ethical approval. However, non–invasive samples were collected as part of a broader study to investigate food resources utilization of the landscape systems by specific bat species. Non–invasive samples included hair clips, faecal and wing biopsy taken from bats which were caught using mist nets and harp traps. Animal ethics approval was therefore acquired from the University of Pretoria Animal Ethics Committee (AEC) and certificate S4285-15 of project number ECO29-17 issued. Land ownership permission was obtained for access to the Savanna (Aquila Steel Pty Ltd and Motjoli Resource) and Grassland (Cradle Farm reserve) study areas. Chapter 3 also adhered to these ethics and permits.

Study Areas

Sampling was undertaken in two karst landscape areas of both Savanna and Grassland biomes. Karst landscapes are dominated by carbonate rocks which can be limestone, dolomite and gypsum (Durand, 2007). Karst systems have biological importance as they support various fauna and flora (Struebig *et al*., 2009). Savanna biome (Figure 1.1) sampling was undertaken from June 2017 to February 2018 at Randestephane 455 KQ farm, within Meletse, Limpopo Province. Meletse lies within the Waterberg Mountain Bushveld and greater Central Bushveld Bioregion (Figure 2.2.2) (Mucina & Rutherford, 2011). Grassland biome (Figure 1.1) sampling was undertaken in 2017 (September and November) and 2018 (January) at the Cradle Farm, within the CoH WHS, Gauteng Province. The CoH WHS forms part of the Carletonville Dolomite Grassland, within the Dry Highveld Grassland Bioregion (Figure 2.2.2) (Mucina & Rutherford, 2011). The South African Savanna and Grassland dry season spans from March/April to September/October whilst wet season span October/November to February/March (Rutherford *et al*., 2006b). Tadross & Hewitson (2005) reported that a minimum of 25mm of rainfall (in the last 10 days) and followed by an accumulation of at least 20mm in the subsequent 20 days is the bare requirement to detect the onset of the rain (wet) season. Using this method, the sampling period here captured wet season from October to February (>45mm per 30 day period) and the dry season from June to September (<45mm per 30 day period). The precipitation thresholds by Tadross & Hewitson (2005) were measured to distinguish wet and dry season at the Meletse study area using a Davis Vantage Vue

Wireless Weather Station (Davis Instruments Corporation, 3465 Diablo Avenue, Hayward, California 94545 USA) based at the Meletse Bat Research and Conservation Training Centre (MBRCTC), Meletse, Limpopo Province.

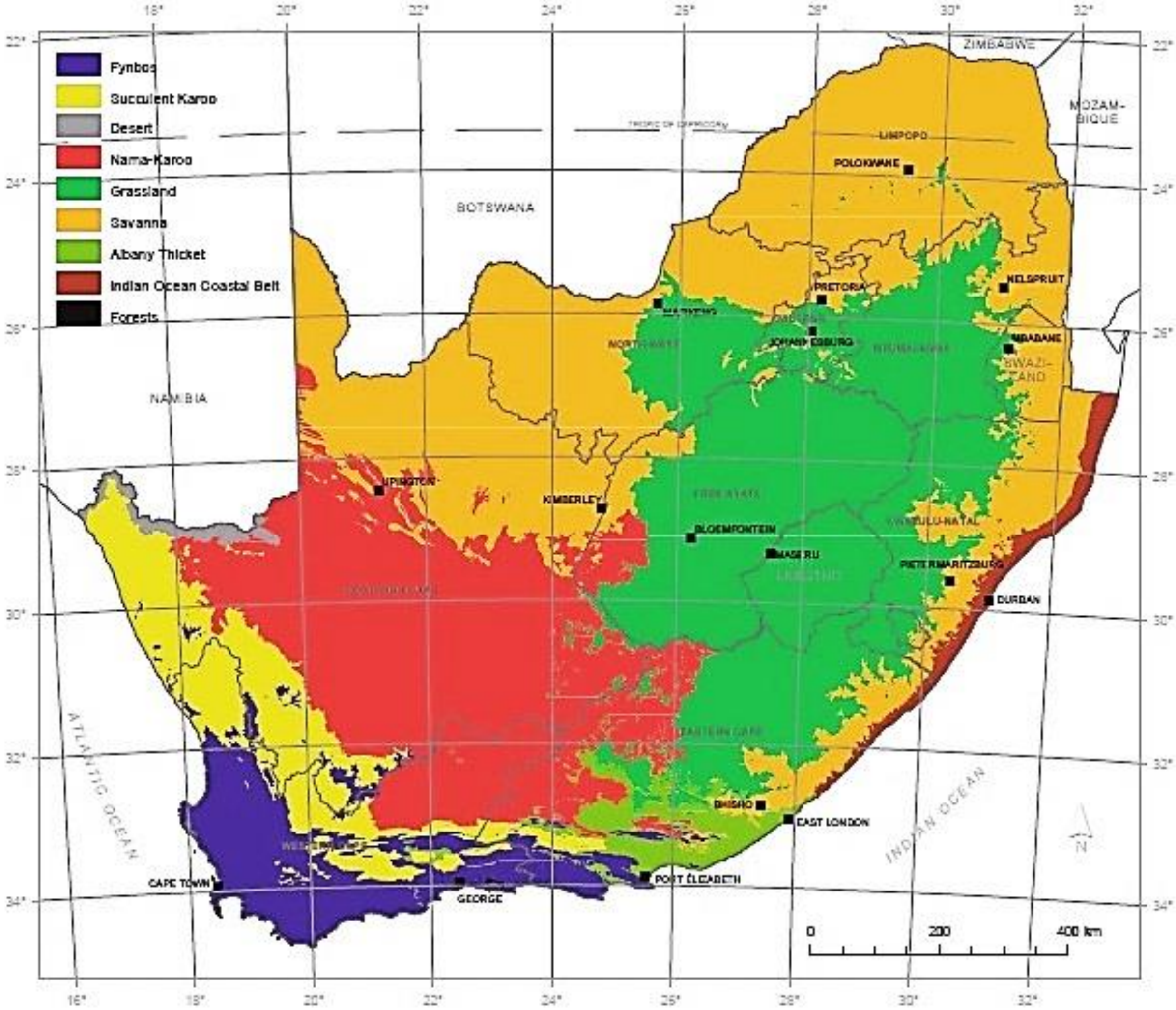

Figure 2.2.1: The different biomes found in South Africa (Rutherford *et al*., 2006b).

Arthropod data collection

Malaise intercept traps (Land and Air Intercept) fitted with trap bottom collectors (Bioquip Products, Inc. 2321 E Gladwic street, Rancho Dominguez, CA 90220) were used to sample nocturnal arthropods (Figure 2.2.3). Pole stands were used anchor both the top and bottom traps as seen in Figure 2.2.3a where no “tree anchorage” was available. Each month, traps were deployed at different levels of vegetation clutter which are explained in the next paragraph.

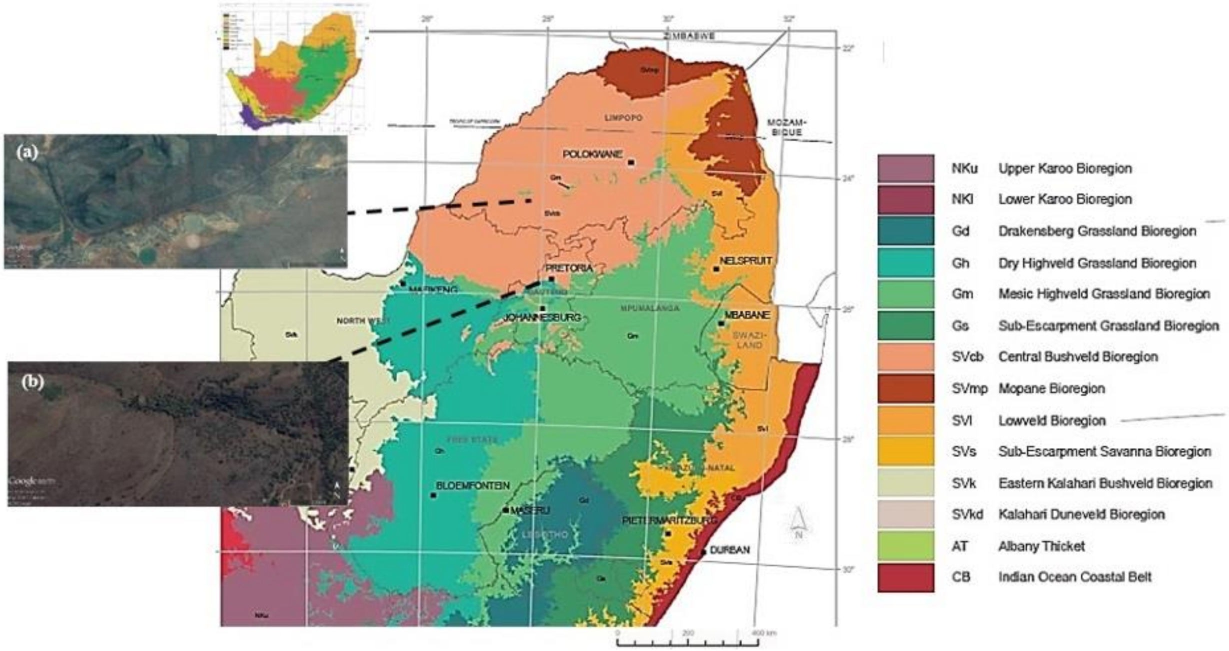

Figure 2.2.2: Bioregions of South Africa (only the easterly portion of the country is shown).Both Meletse and CoH WHS are found on the northern part of South Africa (a) Meletse is found of the Central Bushveld Bioregion (Savanna biome) and (b) CoH WHS is found within the Dry Highveld Grassland Bioregion (Grassland biome) bordering the Mesic Highveld Grassland Bioregion. Map (including insert map) Rutherford *et al*. (2006b). (a) & (b) Google Earth (Accessed 11 August 2017).

The Savanna and Grassland study areas consisted of heterogeneous vegetation structure with varying degrees of clutter. These were defined into three vegetation clutter types (open, edge and closed) by using methods adapted from Law & Chidel’s (2002) vegetation clutter index (VCI). The vertical strata, as defined by VCI, consists of a ground (0.5m<), shrub (0.5m–1m), mid-storey (1m–2m) and maximum (2m and higher) layer. Within each layer quadrate, percentage volume cover estimates are taken. Here, clutter assessment was undertaken within four 2m×2m plots around the malaise trap placed at the centre of a larger 50m×50m plot. The 50m×50m plots for each vegetation clutter type were separated by a buffer distance greater than 50m (Figure 2.2.4).

Open vegetation clutter was defined as having a mid-storey clutter of less than 10% and maximum clutter of more than 10%. Closed vegetation clutter consisted of mid-storey and maximum vegetation clutter above 50% and 70%, respectively. The edge vegetation clutter type was therefore defined as an area along the boundary of defined open and closed clutter types. Percentage volume cover along the edge varied according to density of vegetation. Acceptable

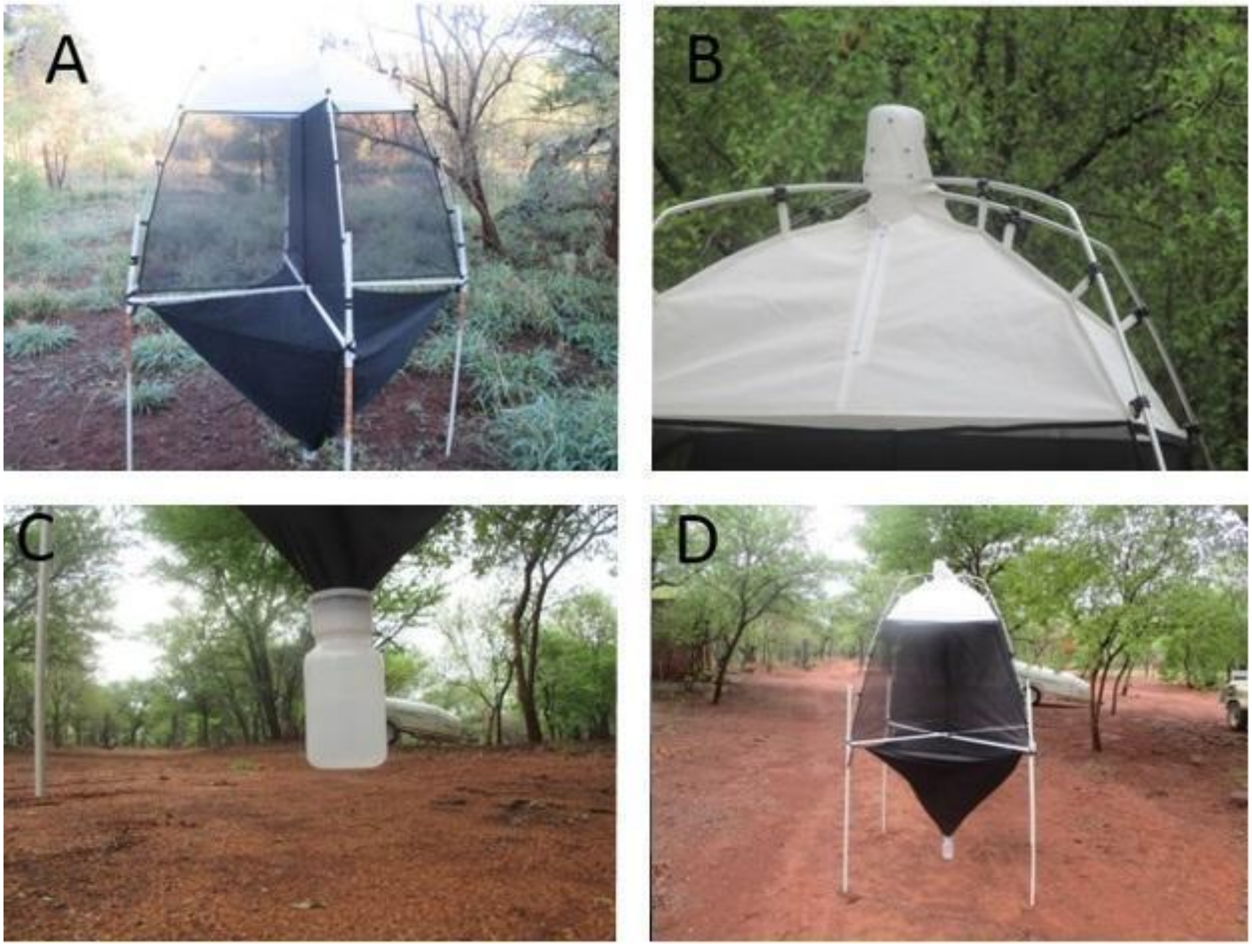

Figure 2.2.3: Malaise intercept trap deployed in the field. (a) A special PVC frame was designed and constructed to allow for deployment in open areas that lack tree anchorage. (b) Top collecting section collected arthropods which flew up in the jar (beneath the zipper). (c) Bottom collecting section collected falling arthropods in the connected jar. (d). Malaise intercept trap with top and bottom jars connected. The top trap has four panels which intercept at the centre.

ranges were between 10% and 50% mid–storey maximum clutter below 10% vegetation clutter. Although the percentage classes for assessing clutter were adapted from Law & Chidel (2002), that study did not classify space as open, edge or closed.

Malaise intercept traps were placed in open, edge and closed vegetation clutter types (Figure 2.2.5 & Figure 2.2.6). Comparisons of arthropod data at vegetation clutter level was only considered for the Savanna as sampling spanned both dry and wet seasons. Grassland sampling was undertaken, to a great extent, in the wet season. Furthermore, traps were deployed at night to bias for nocturnal arthropods which form the main diet of their nocturnal predators (Cleveland *et al*., 2006; Findley

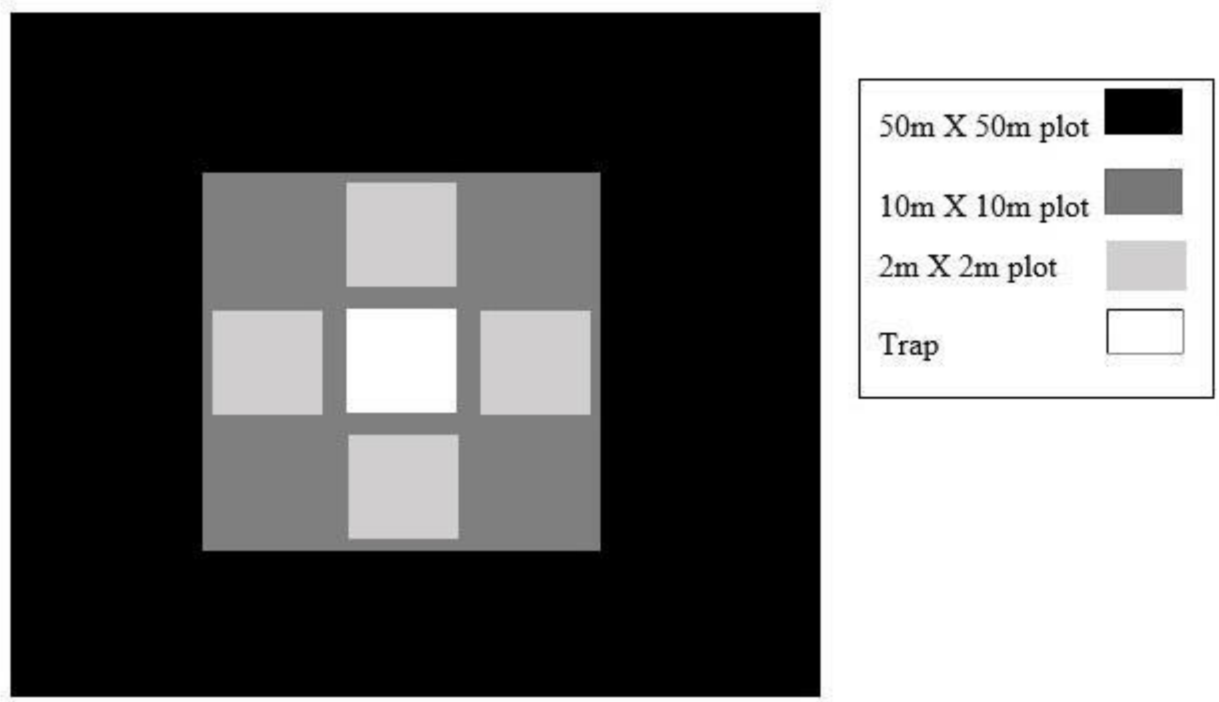

Figure 2.2.4: Plot of 50m×50m area in which vegetation clutter type was defined; 10m×10m plot: Square plot cluttering the centre; 2m×2m plots: Square area where vegetation clutter assessment was undertaken, following methods adapted from Law & Chidel (2002); Trap plot: Malaise trap deployment site at the centre.

& Black, 1983; Whitaker, 1995). Ethyl acetate (immobilising agent) was used to activate traps at a standardized two hours before sunset and ceased within 30 minutes after sunrise. Each trap has four capture panels measuring 0.8m by 0.5m (height and width) which provides a 1.6m2 capture area for each trap panel. The capture effort, capture area multiplied by duration (hours) traps are activated (Esberard, 2009), was obtained for each month and per trap (Table A.1c), subject to standardized times. Capture effort was standardized between the two study areas by using three traps at Meletse (ten nights) and five traps at CoH WHS (six nights). Capture success (CS), calculated as number of individuals (ind.) caught divided by capture effort (trap-hours), was determined for the duration that traps were activated and expressed to the nearest three decimals (Table A.1).

Arthropod count and biomass

Food source availability in the sampled areas was equated to arthropod abundance, biomass and taxonomic order proportion across the time this research took place. Arthropod abundance refers

Figure 2.2.5: Ranstephane 455KQ property at Meletse (Savanna), Limpopo Province, South Africa. Each red line represents a >100m buffer between each trap belonging to a trap line. The black, pink and green blocks represent closed, edge and open vegetation clutter types, respectively. Malaise traps were deployed at the centre of each plot. (Google Earth, Accessed 11 August 2017).

to the number of individuals collected per night whilst biomass is the measured dry weight of all these arthropod individuals. Collected arthropods were counted on a white tray for better visibility. A magnifier head strap, with a double lens, and an LED light (Magnifier Head Strap with Lights, MG81007), was used to count and identify small arthropods (usually <4mm) which were otherwise inconspicuous to the naked eye. Individuals which required a higher magnification were marked and later viewed and identified using a compound light microscope (Zeiss Stemi DV4/DR Microscope Stereo). Reference material (Davis *et al*., 2008; Scholtz & Holm, 1985; Smith, 2008) were used for identifying the arthropods to order level. In addition, a separate category called 'unidentifiable' was created for arthropods which could not be identified. Each sample was sorted based on vegetation clutter type (open, edge, closed), date, and taxonomic order.

This counting process was repeated for the duration of each sampling event throughout this study. Collected arthropods from each sampling event were oven dried (Memmert, GmBh + Co.KG, Aeussere Rittersbacher, Strasse 38, D-91126 Schwabach), for 15 hours at 60˚C to obtain their biomass from dry weight. Biomass of species is better determined from dry weight as it reduces

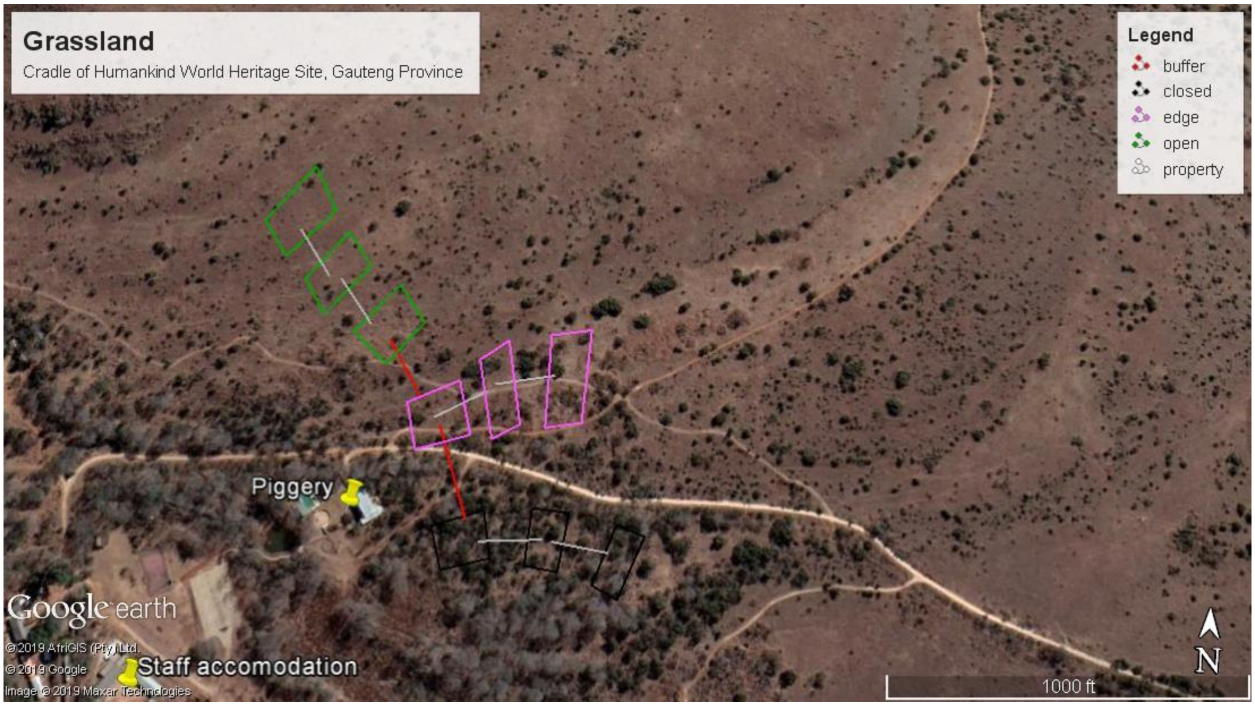

Figure 2.2.6: Cradle Farm property at CoH WHS (Grassland), Gauteng Province, South Africa. Black, pink and green blocks represent closed, edge and open vegetation clutter types, respectively. Traps were deployed at the centre of each plot. The red lines represent >100m buffers between each vegetation assessment plot whilst light grey lines represent >50m distance between traps that were deployed in the same vegetation clutter type in the sampling event. (Google Earth, Accessed 11 August 2017).

variations caused by water content in the case of fresh weight (Gilbert, 2011). Dried arthropods were categorized into distinct size classes with the aim of comparing temporal proportion of each size group in terms of biomass and abundance. Size classes consisted of A, B, C, D and E and distinguished by length and width. Dimensions for each size class are as follows: A (<4.5mm×2.6mm), B (<12.5mm×3.5mm), C (<17.8mm×5.7mm), D (18.1mm×9.5mm) and E (30.3mm×6.4mm). For each size class, at least 30 individual arthropods were measured (except D and E where fewer arthrpods were caught). The dry weight of each size category was measured using an electric balance with a three decimal (0.000) accuracy (Chyo Electric Balance, JP-2-160, Chyo Balance Corpration, Kyoto, Japan). Size categories were based on distinguished groupings of length vs width.

Data analysis

Non–parametric tests were used as Shapiro –Wilk's test showed non-normality for all arthropod count data (($p<0.01$). Kruskal-Wallis ANOVA and a subsequent Post-hoc Dunn test were used to compare arthropod count data from Savanna across sampled months and vegetation clutter types. A monthly comparison of Savanna vs Grassland arthropod count data was done using a Mann-Whitney U-test. All analysis was performed using R (version 3.1.2, 2014) with scripts developed using the programs RStudio and R Commander (Fox, 2005). The minimum (min), maximum (max), mean, standard deviation (SD) and variance of collected arthropods were calculated for each vegetation clutter type across sampled months.

2.3: Results

Savanna temporal food resource availability: arthropod abundance, biomass and taxonomic order proportions

During this study, 3418 arthropod individuals (ind.) representing 15 taxonomic orders were collected over the period of nine months spanning the dry to wet season. Most of the arthropod abundance (80%) and biomass (68%) were collected in the wet season (October to February). The range (minimum–maximum), mean and standard deviation are reported (Table A.4). There was significant difference (Kruskal-Wallis ANOVA: $n=270$, $\chi2 = 46.33$, $d.f = 8$, $P < 0.01$) between combined (sum of open, edge and closed) monthly samples. Dry season (June to September) combined nightly captures (Figure 2.3.1i) were lower although a season peak was observed in August (range: 11–52 ind., mean = 36 ind., SD = 13.01– Table A.4, *Z. stat* = 2.65, P = 0.004 - Table A.2a). Biomass peaked in September at 1.41g (Table 2.3.1), which was half the value observed in August (0.71g, Table 2.3.1), even though captures were lower (range: 14–46 ind., mean = 30 ind., SD = 10.83– Table A.4) than August.

Combined capture success (CS), (Table A.1a) for the orders Coleoptera, Diptera, Hemiptera, Hymenoptera and Lepidoptera were 0.013, 0.005, 0.022, 0.003, and 0.072 ind. /trap-hours, respectively, in August. Large differences in CS were observed in October for Coleoptera (0.028 ind. /trap-hours), Hemiptera (0.035 ind. /trap-hours) and Lepidoptera (0.017 ind. /trap-hours). In November, a peak in the combined arthropod abundance (range: 2–158 ind., mean = 69 ind., SD = 50.02, Table A.4) and biomass (4.47g, Table 2.3.1) was observed following a significant increase (*Z. stat* = 2.73, P = 0.0031, Table A.2a) from October. Notable peaks in CS were observed for Coleoptera (0.084 ind. /trap-hours) and Hymenoptera (0.093 ind. /trap-hours) and Isoptera (0.015 ind. /trap-hours) in November (Table A.1a). Infraorder Isoptera (order Blattodea) was only recorded in November. Generally, a decreasing trend was observed for most orders from November to February (Table A.1a). A gradual decrease in arthropod abundance (Figure 2.3.1i) was observed in December (range: 22–136 ind., mean = 61 ind., SD = 33.81, Table A.4), January (range: 14–100 ind., mean = 44 ind., SD = 27.23, Table A.4) and February (range: 16–60 ind., mean = 35 ind., SD = 13.25, Table A.4) as shown in Table A.1a. Meanwhile, arthropod biomass reduced by more than half (Table 2.3.1) for December, January and February, as compared to the November peak.

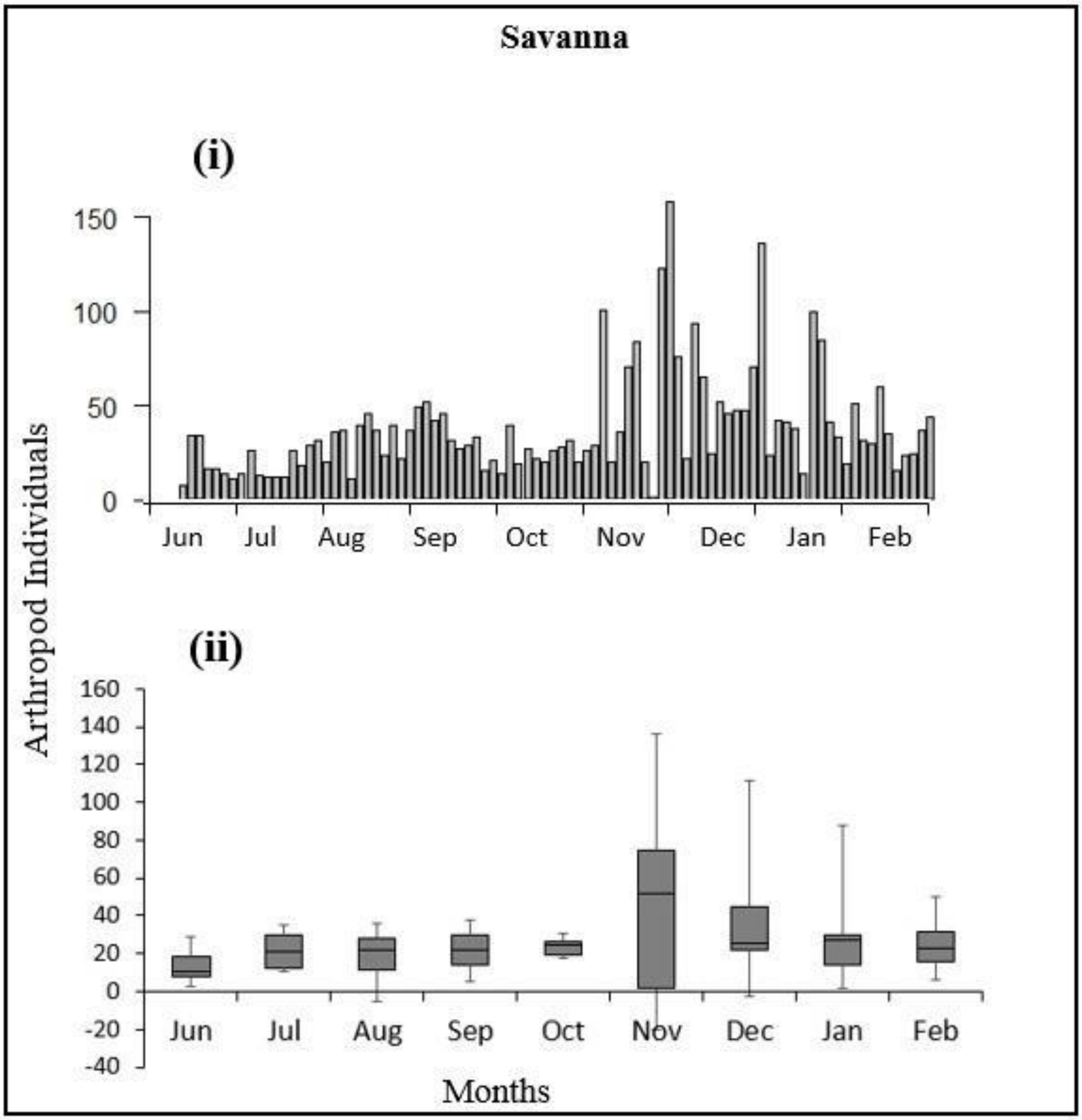

Figure 2.3.1: (i) Nightly arthropod abundance and (ii) monthly boxplots of arthropod captures from June 2017 to February 2018 in the Meletse (Savanna), Limpopo Province area, South Africa.

Arthropod size proportion percentages were calculated based on monthly abundance and biomass of each size class (Table 2.3.2). Measurement differences in length and width between the size class categories were significantly different (width–P < 0.01; length–P < 0.01). In the combined samples, the size class A (smallest class) was the highest in terms of abundance across all months (Figure 2.3.2i) with proportions remaining above 66% throughout (Table 2.3.2). In addition, lower proportions were observed for size classes B (26%), C (8%), D and E (2%, both). Arthropod biomass size proportions were contrastingly higher for the larger size classes making up to 56% (B), 70% (C), 37% (D) and 49% (E) whilst size class A proportions were lowest at 32%.

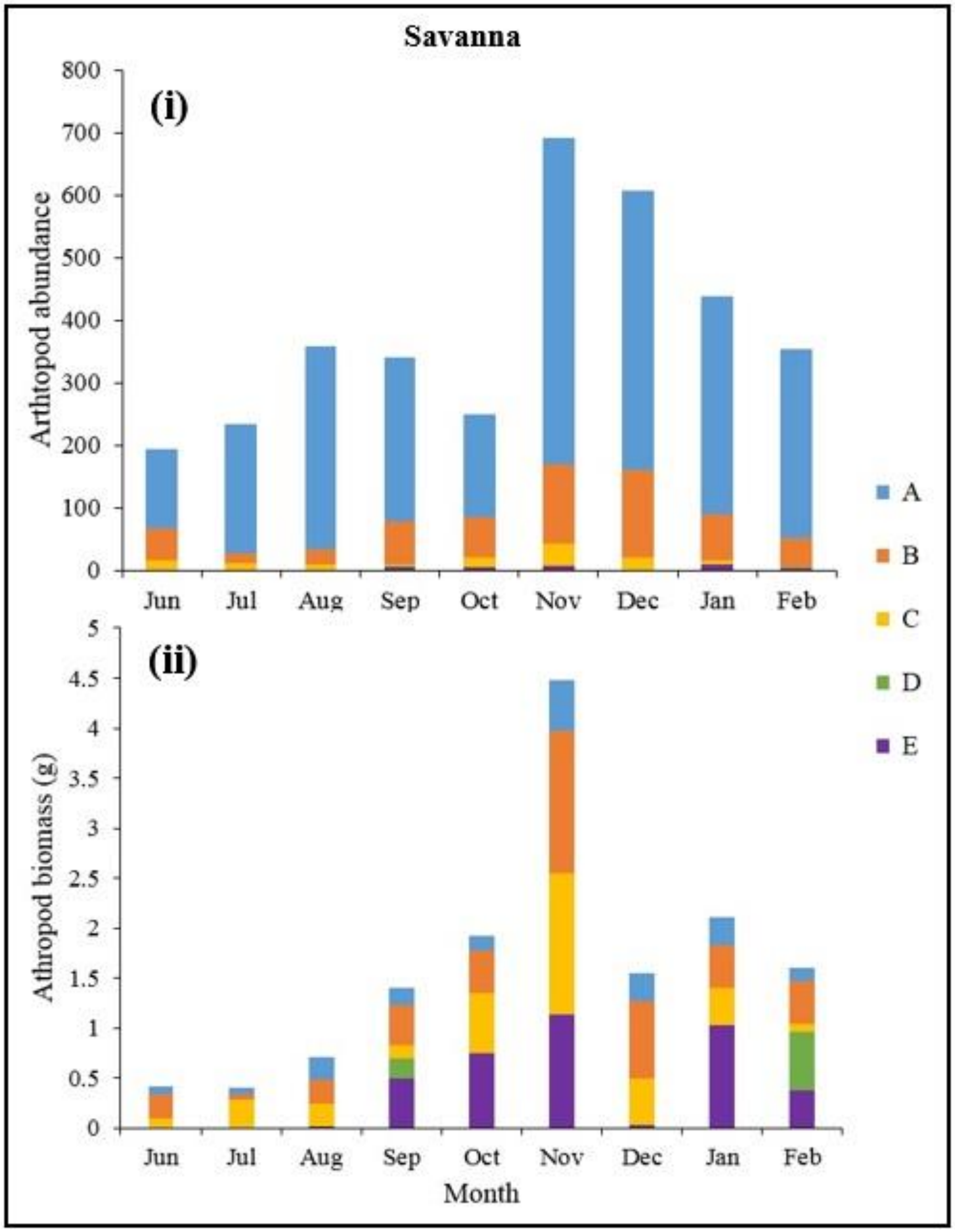

Figure 2.3.2: Monthly arthropod size (i) abundance and (ii) biomass. Collected arthropods were placed into size classes A (<4.5x2.6mm), B (<12.5x3.5mm), C (<17.8x5.7mm), D (18.1x9.5mm) and E (30.3x6.4mm). Combined (i) monthly abundance and (ii) biomass of each size class collected at the Meletse (Savanna), Limpopo Province, South Africa.

In June (lowest observed abundance – Table A.4), size biomass proportions were 20%, 56% and 23% size classes A, B and C, respectively (Table 2.3.2). In September, when observed biomass increased (Table 2.3.1), size biomass proportions were 13% for smallest size (A) and 35% for largest size (E). Biomass proportions for the intermediate size classes B, C and D were 28%, 9% and 15%, respectively, in September. In the peak month of November, size biomass proportions remained higher for the larger sized arthropods (A = 11%; B = 32%; C = 32%; E = 25%, Table 2.3.1). In January, observed arthropod biomass (Table 2.3.1) was higher despite a lower abundance and mean (Table A.1a and Table A.4) as compared to December. Size biomass proportions for that month (January) were 13% (A), 20% (B), 17% (C) and 49% (E), as seen in Table 2.3.1.

Table 2.3.1: The actual monthly biomass (g) values of collected arthropods from Meletse (Savanna), Limpopo Province (collected from June 2017 to February 2018), and CoH WHS (Grassland), Gauteng Province (collected September and November 2017, and January 2018), South Africa Arthropods from Meletse and CoH WHS are sorted into combined captures whilst the former is further sorted across vegetation clutter types.

	Combined	Open	Edge	Closed
		Meletse		
Jun	0.42	0.07	0.22	0.12
July	0.41	0.09	0.10	0.22
August	0.72	0.21	0.27	0.24
September	1.41	0.19	0.99	0.23
October	1.93	0.28	0.83	0.82
November	4.47	2.75	0.76	0.96
December	1.55	0.62	0.52	0.41
January	2.11	0.80	0.21	1.10
February	1.61	1.28	0.24	0.09
Total	14.61	6.28	4.14	4.19
		CoH WHS		
September	1.87			
November	1.33			
January	2.98			
Total	6.19			

Savanna taxonomic order proportions

Collected orders included Acari and Aranea (class Arachnida), Blattodea (including infraorder Isoptera), Coleoptera, Dermaptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Mantodea, Mecoptera, Neuroptera, Orthoptera, Raphidoptera and Siphonaptera. Arthropods which could not be identified were labelled ‘unidentifiable’. Of all the 15 collected taxonomic orders, only six comprised more than 1% of combined capture proportions (Table A.3). These included Arachnida (3%), Coleoptera (27%), Diptera (6%), Hemiptera (14%), Hymenoptera (20%) and Lepidoptera (27%). In the first sample (June), arthropod captures consisted largely of Coleoptera and Lepidoptera (38% and 36%, respectively) while Arachnida, Diptera, Hemiptera and Hymenoptera made up 3%, 10%, 5%, and 2%, respectively. The proportion of Coleoptera decreased to 11% in August and then increased to 15%, 29% and 32% in September, October and November, respectively. Lepidoptera proportions increased to 58% in August and dropped in the following months (September = 37%, October = 18%, November = 18%, December =18%). Similarly, the proportion of Hemiptera decreased in the November to February period as opposed to higher, and ascending proportions in previous months (June to October). During the period from November to February, a shift in taxa proportion occurred where in Hymenoptera comprised larger portions of the sample. Sample proportions from November to February averaged 21% for Hymenoptera as opposed to an average of 3% from June to September (Table A.3). A decreasing trend in arthropod abundance occurred from November till February (significant in December: $P < 0.01$ and February–$P < 0.0001$). During the same period, an upward trend in biomass was observed from December to February (Table 2.3.1).

Savanna comparison of food resource availability between vegetation clutter types: arthropod abundance, biomass and taxonomic order proportion

Wet season arthropod compositions were as follows: open (76% abundance and 91% biomass), edge (63% abundance and 62% biomass), closed (63% abundance and 81% biomass). For the open vegetation clutter type, arthropod captures were highest and most spread out (n = 90, mean = 16 ind., SD = 16.07, variance = 258.27, Table A.4). Furthermore, dry season captures were lowest in June (range: 1–11 ind., mean = 6 ind., SD = 2.31, biomass = 0.07g, Table A.4; Table 2.3.1). Captures thereafter showed little, non-significant changes with the following Post-hoc Dunn test scores (n =90): (July - *Z. stat* = 0.65, P = 0.26, Table A.2b), August (*Z. stat* = 1.06, P = 1.06, Table A.2b), September (*Z. stat* = 0.31, P = 0.38, Table A.2b), October (*Z. stat* = -1.41, P = 0.08, Table A.2b). In November, a significant increase in arthropod captures occurred (n = 90, *Z. stat* = -2.35, $P < 0.01$; mean = 35 ind., SD = 30.30, Table A.2b, Table A.4a) with biomass about 38 times (2.75g) greater than observed in June (Table 2.3.1).

Table 2.3.2: Arthropod size proportions % (abundance | biomass) for Meletse (Savanna), Limpopo Province (June 2017 to February 2018) and CoH WHS, Grassland, Gauteng (September, November 2017 and January 2018). Combined size proportions are given for Meletse and CoH WHS (indicated with *) whilst the former is further categorized by vegetation clutter type. Size classes - A (<4.5mm×2.6mm), B (<12.5mm×3.5mm), C (<17.8mm×5.7mm), D (18.1mm×9.5mm) and E (30.3mm×6.4mm).

	June	**July**	**August**	**September**	**October**	**November**	**December**	**January**	**February**
					A				
*Combined COH WHS				73|14		86|16		58|9	
Combined	66|20	89|19	91|32	77|13	66|8	76|11	74|18	80|13	85|9
Open	62|34	86|19	90|31	82|36	79|22	75|7	83|19	82|12	80|4
Edge	60|15	88|22	86|24	69|5	64|5	83|20	70|17	88|24	89|16
Closed	77|21	91|18	95|41	80|26	51|7	71|17	55|18	74|13	90|55
					B				
*Combined				20|26		12|21		39|34	
Combined	26|56	6|11	7|34	20|28	27|22	18|32	23|50	16|20	13|26
Open	31|57	9|19	5|11	16|38	19|46	16|21	14|45	15|17	17|20
Edge	28|45	6|18	11|31	25|21	19|6	14|34	26|55	9|27	11|50
Closed	18|79	4|4	5|59	19|51	40|30	26|62	40|51	21|22	10|45
					C				
*Combined COH WHS				5|36		2|39		1|12	
Combined	8|23	5|70	2|31	1|9	6|31	5|32	3|30	2|17	0|5
Open	7|9	5|63	5|58	1|11	1|21	7|31	2|36	1|7	0|0
Edge	13|40	5|60	3|38	2|5	13|34	4|45	4|28	2|49	1|34
Closed	5|0	4|78	0|0	1|23	8|31	3|21	4|23	3|19	0|0
					D				
*Combined COH WHS				0|0		1|24		0|0	
Combined	0|0	0|0	0|0	1|15	0|0	0|0	0|0	0|0	0|37
Open	0|0	0|0	0|0	0|0	0|0	0|0	0|0	0|0	1|46
Edge	0|0	0|0	0|0	2|21	0|0	0|0	0|0	0|0	0|0
Closed	0|0	0|0	0|0	0|0	0|0	0|0	0|0	0|0	0|0
					E				
*Combined COH WHS				1|24		0|0		2|45	
Combined	0|0	0|0	0|3	1|35	2|39	1|25	0|2	2|49	1|24
Open	0|0	0|0	0|0	1|15	1|10	2|41	0|0	2|64	2|30
Edge	0|0	0|0	1|8	3|47	4|55	0|0	0|0	0|0	0|0
Closed	0|0	0|0	0|0	0|0	1|33	0|0	1|9	3|47	0|0

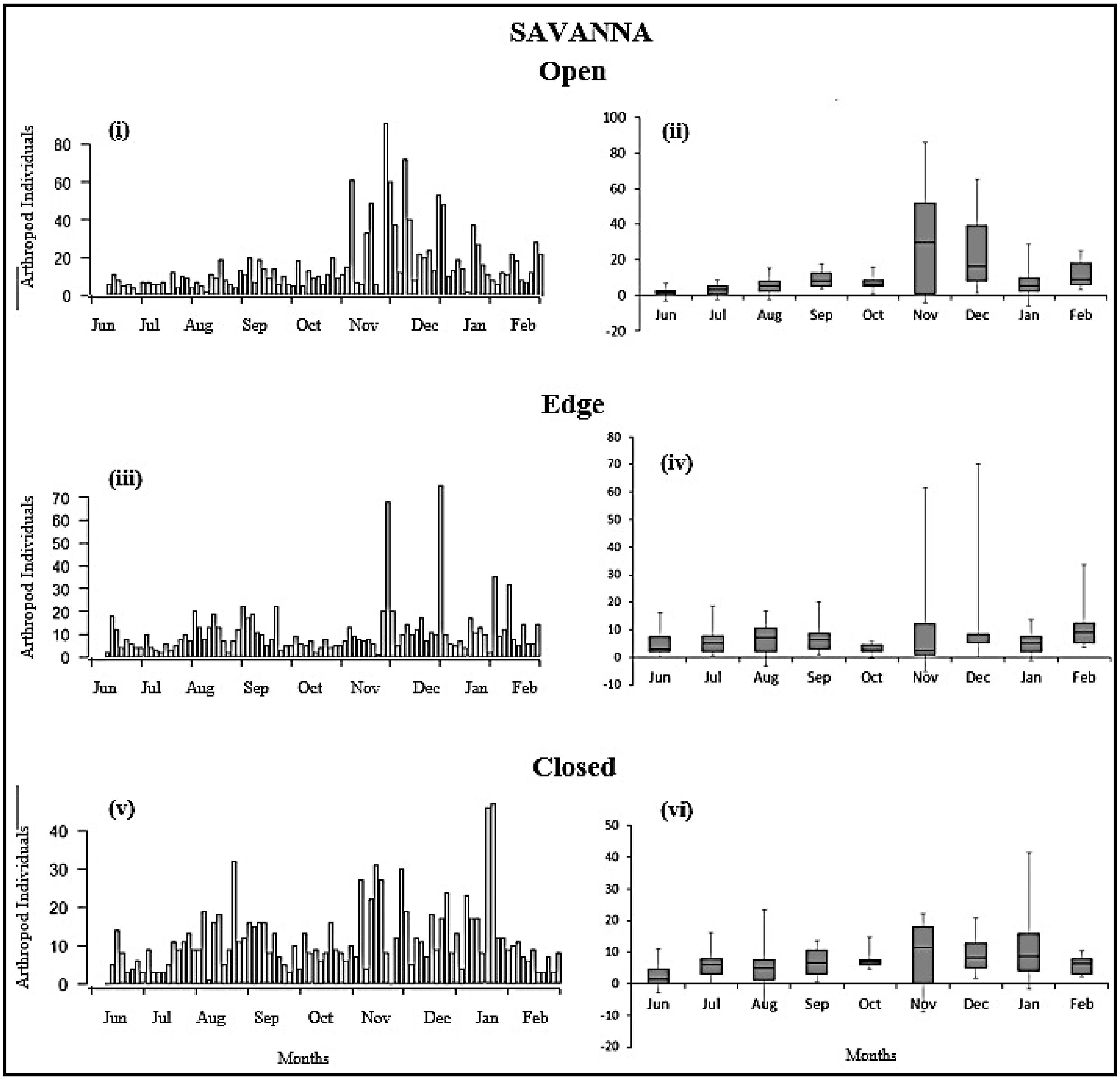

Figure 2.3.3: Arthropod captures (June 2017 to February 2018) from the Meletse (Savanna), Limpopo Province study area collected at (i) open, (iii) edge and (v) closed vegetation clutter types. Box plots of arthropod captures from (ii) open, (iv) edge and (vi) closed vegetation clutter types. Q2 at the open (ii) showed the most variation in November and December relative to all other months. Meanwhile, Q2 values at the edge showed the least deviation relative to open and closed throughout the sampling period.

The edge vegetation clutter type (Figure 2.3.3iii and iv) yielded a lower number of arthropod captures which were less spread out from the mean (n = 90, mean = 11 ind., SD = 11.04, variance = 121.95, Table A.4). Changes in arthropod captures during the dry season fluctuated significantly with an increase in Augusts (n =90, *Z. stat* = -2.67, P < 0.02, Table A.2c) followed by a decrease in September (n =90, *Z. stat* = 2.97, P < 0.01, Table A.2c). A decrease occurred in October (n = 90, *Z. stat* = -2.67, P < 0.01, Table A.2c) the lowest recorded capture (mean = 5 ind., SD = 4.36, Table A.4). In November, arthropod captures increased, although non–significantly (*Z. stat* = -0.06, P = 0.47, mean = 16 ind., SD = 19.23, Table A.2c, Table A.4). Between November and February, an oscillating trend was observed with non-significant scores in December (n = 90, *Z. stat* = 0.16, P = 0.44, Table A.2c), January (n = 90, *Z. stat* = -0.72, P = 0.24, Table A.2c) and February (n = 90, *Z. stat* = 1.16, P = 0.12, Table A.2c). Biomass increased three times higher in September (0.99g) and change remained within ±0.3g range till December (Table 2.3.1).

Table 2.3.3: Monthly precipitation (total) and temperature (minimum, maximum and mean) split into dry (June to September, 2017) and wet (October 2017 to February 2018) seasons measured on the Davis weather station at Meletse (Savanna), Limpopo Province.

	Total precipitation (mm)	**Temperature (˚C)**		
		Maximum	**Minimum**	**Mean**
Dry season				
June	0	25	5.3	14.8
July	2.8	25.2	6.2	15.5
August	0	26.7	8.1	17.6
September	0.6	32.3	14.7	23.5
Wet season				
October	52.8	31.5	15.3	23.7
November	77.8	32.9	16.4	24.9
December	104.2	32.6	18.2	25.3
January	91	35	19.3	26.7
February	107.6	30.2	18.5	23.6

Arthropod captures from the closed vegetation clutter type (Figure 2.3.3v and vi) displayed the least spread and combined abundance (n = 90, mean = 11 ind., SD = 8.66, variance = 75.05, Table A.4). Captures were lowest in June (mean = 6 ind., SD = 4.85, Table A.4) and increased significantly in the latter part of the dry season in August (*Z. stat* = -1.72, P = 0.04, mean = 14 ind., SD = 4.85, Table A.2d, Table A.4). In the wet season, increases were seen in the November and January with the latter being significant (*Z. stat* = 3.00, P < 0.01, mean = 20 ind., SD = 2.95, Table A.2d, Table A.4). Also in the wet season, non-concurrent and significant decreases occurred in arthropod captures in October (*Z. stat* = 1.65, P < 0.05, Table A.2d, mean = 9 ind., SD = 11.29, Table A.4), December (*Z. stat* = -1.76, P = 0.04, mean = 12 ind., SD = 15.2, Table A.2d, Table A.4) and February (*Z. stat* = -1.88, P = 0.03, mean = 7 ind., SD = 8.71, Table A.2d, Table A.4) which made a fluctuating trend in arthropod captures. For biomass, less variation was observed in the dry season which kept within the 0.2g (±0.1g) range. A fourfold increment was observed in the beginning of the wet season in October (0.82g, Table 2.3.1). Biomass kept within the 0.82g (±0.3g) range in November and January (Table 2.3.1). Within the wet season, specifically in December and February, decreases in biomass occurred at 0.41g and 0.09g, respectively (Table 2.3.1). When comparing mean arthropod abundance and biomass in the November peak event, the open (mean = 35 ind., 2.75g, Table A.4, Table 2.3.1) had higher scores than edge (mean = 17 ind., 0.99g, Table A.4, Table 2.3.1) and closed (mean = 20 ind., 1.1g, Table A.4, Table 2.3.1). Despite edge and closed vegetation clutter types having similar abundance peaks with mean captures of 16 and 18, respectively, edge had more variability in nightly captures. In terms of biomass, an earlier peak was seen for the edge in the dry season (September–0.99g, Table 2.3.1) whilst abundance wet season peaks occurred for the open (November–2.75g, Table 2.3.1) and closed (January–1.1g, Table 2.3.1).

In terms of size proportions, arthropods belonging to size class A dominated captures by making up more than 50% of abundance across all vegetation clutter types from June to February (Table 2.3.2). Meanwhile, all the size classes were fairly reflected in terms of biomass proportion.

Grassland food resource availability: arthropod abundance, biomass and size proportions

A total of 1948 individual arthropods from 13 taxonomic orders were collected at the Grassland over the late dry to wet season period. Collected taxa include class Arachnida (orders Acari and Araneae), Blattodea, Coleoptera, Dermaptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Mecoptera, Mantodea, Orthoptera, and Raphidoptera. Across the three sampled months, only five taxonomic orders made up a hundredth (CS>0.01 ind. /trap-hours) or more of captures whilst the rest were lower: Coleoptera (0.040 ind. /trap-hours, Table A.1b), Diptera (0.022 ind. /trap-hours, Table A.1b), Hemiptera (0.043 ind. /trap-hours, Table A.1b), Hymenoptera (0.012 ind. /trap-hours, Table A.1b) and Lepidoptera (0.117 ind. /trap-hours, Table A.1b). Furthermore, Lepidoptera had the highest CS throughout the three sampling events which remained above 0.100 ind. /trap-hours (Table A.1b). In September (Table A.1b) the orders Coleoptera (CS = 0.013 ind. /trap-hours), Diptera (CS = 0.008 ind. /trap-hours), Hemiptera (CS =0.022 ind. /trap-hours) and Hymenoptera (CS = 0.007 ind. /trap-hours) had CS five times less than Lepidoptera (CS = 0.114 ind. /trap-hours).

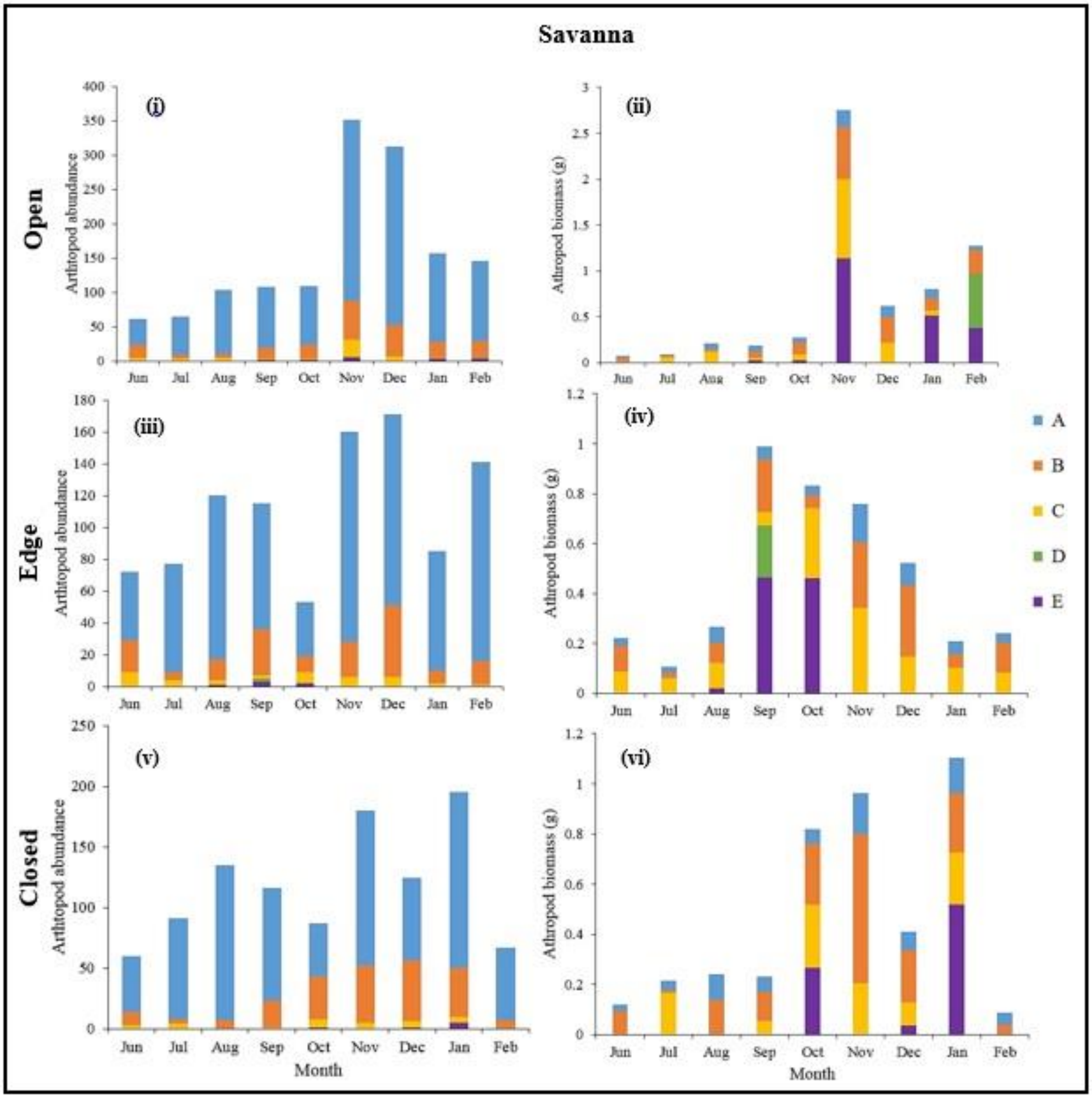

Figure 2.3.4: Arthropods ind. sampled at Meletse (Savanna), Limpopo Province sorted per size class abundance proportion from (i) open, (iii) edge and (v) closed vegetation clutter types, and size class biomass proportions from the (ii) open, (iv) edge and (vi) closed vegetation clutter types.

In the following sampling month of November (Table A.1b), captures for Coleoptera (CS = 0.065 ind. /trap-hours), Diptera (CS = 0.046 ind. /trap-hours) and Hemiptera (CS = 0.047 ind. /trap-hours) increased substantially despite being less than Lepidoptera (CS = 0.106 ind. /trap-hours) captures. In January (Table A.1b), Coleoptera and Hemiptera retained heightened CS of 0.045 and 0.065 ind. /trap-hours, respectively, whilst Diptera (CS = 0.015 ind. /trap-hours) decreased and

Hymenoptera (CS = 0.021 ind. /trap-hours) increased. Meanwhile, Lepidoptera (CS = 0.132 ind. /trap-hours) peaked in January (Table A.1b).

The highest number of arthropods were collected in November and January which had similar CS (0.282 and 0.290 ind. /trap-hours, respectively, Table A.1b) and the same mean of 24 ind. (Table A.1b, Table A.4). Arthropod abundance was not statistically significantly different (Kruskal-Wallis ANOVA: n=90, $\chi2$ = 5.89, d.f = 2, P = 0.05) across the three sampled months (September December and January). Despite having a similar number of caught arthropods, biomass in January (2.98g) was more than twice the recorded mass in November (Table 2.3.1). In addition, biomass from September was higher than November albeit higher mean and CS in the latter month (Table 2.3.1, Table A.1b and Table A.4). From a size perspective, the smallest arthropods (size A) made up the bulk of abundance proportions (September = 73%, November = 86%, January = 58%, Table 2.3.2). Size biomass proportions, however, consisted more of the larger size classes in September (B = 26%, C = 36%, E = 24%, Table 2.3.2), November (B = 21%, C = 39%, D = 24%, Table 2.3.2) and January (B =34%, C =12%, E = 45%, Table 2.3.2).

A comparison between CoH WHS and Meletse for the months of September, November and January shows that the former yielded higher arthropod availability. Differences in arthropod availability were more apparent in terms of abundance especially in September (Grassland: 494 ind., Savanna: 300 ind.; n =30) and January (Grassland: 724 ind., Savanna: 437 ind.). Meanwhile, arthropod biomass was slightly higher at CoH WHS than Meletse for September (Grassland: 1.87g, Savanna: 1.41g, Table 2.3.1) and January (Grassland: 2.98g, Savanna: 2.11g, Table 2.3.1). A smaller difference in arthropod abundance was observed in the peak month of November (Grassland: 730 ind., Savanna: 691 ind.) although biomass was more than three times greater at Meletse (4.47g, Table 2.3.1) than CoH WHS (1.33g, Table 2.3.1). In addition, there were slight differences in the biomass proportion of larger sized arthropods at Meletse (A = 11%, B =32%, C = 32%, E = 25%, Table 2.3.2) compared to CoH WHS (B = 21%, C = 39%, D = 24%, Table 2.3.2). At order level, the following CS values were observed at CoH WHS (Table A.1b): Coleoptera (CS = 0.065 ind. /trap-hours), Diptera (CS = 0.046 ind. /trap-hours), Hemiptera (CS =0.047 ind. /trap-hours), Hymenoptera (CS = 0.009 ind. /trap-hours) and Lepidoptera (CS = 0.106 ind. /trap-hours), in November. In contrast, at Meletse (Table A.1a), lower CS were recorded for Diptera (CS = 0.003 ind. /trap-hours), Hemiptera (CS = 0.012 ind. /trap-hours) and Lepidoptera (CS = 0.049 ind.

/trap-hours) whilst Coleoptera (CS = 0.084 ind. /trap-hours) and Hymenoptera (CS = 0.093 ind. /trap-hours) were relatively higher than recorded at CoH WHS for November.

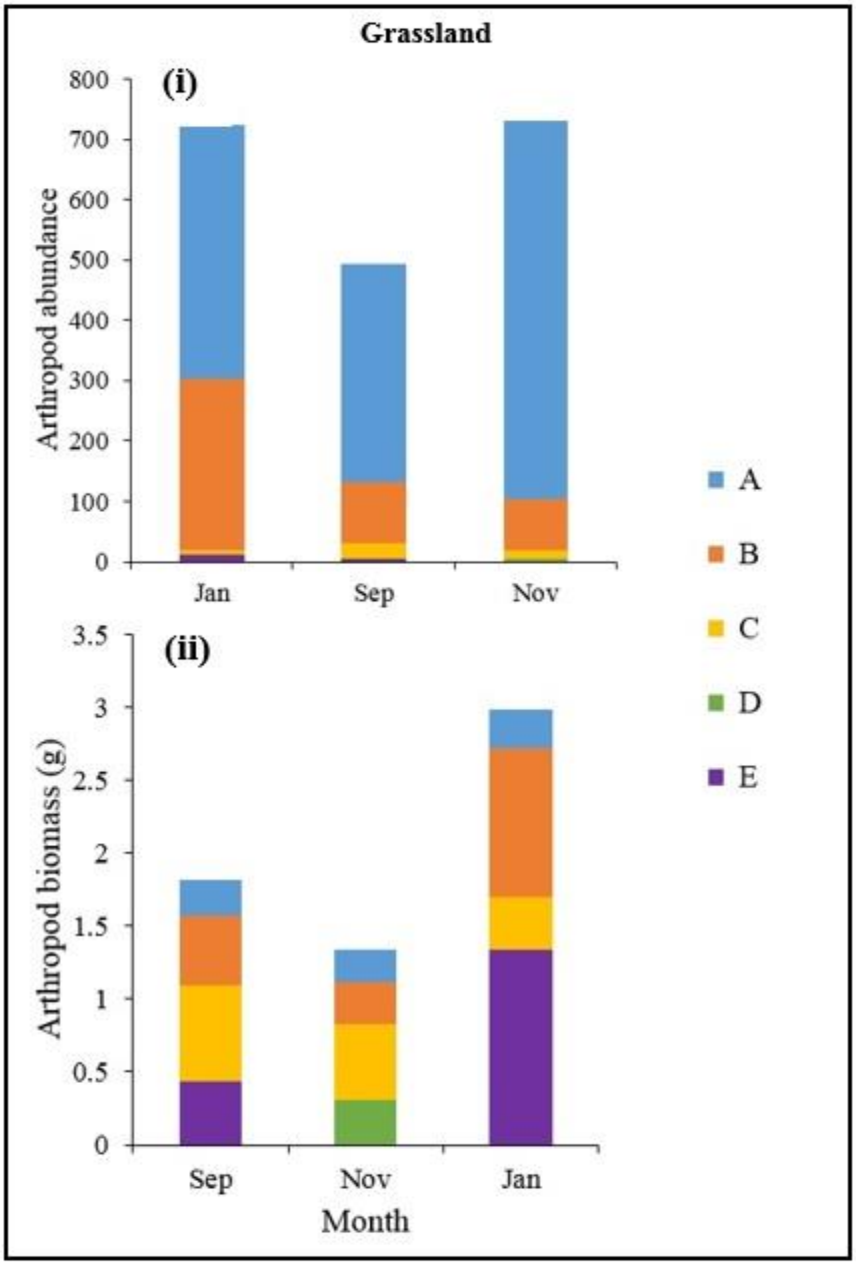

Figure 2.3.5: Arthropod size (i) abundance and (ii) biomass for September 2017 and November 2017 and January 2018 collected from the, CoH WHS, Grassland, Gauteng Province, South Africa.

Statistically, arthropod abundance was significantly higher at CoH WHS than Meletse for September (Mann-Whitney two sample test: n =60; W=711; P = 1.14e-04) and January (Mann-Whitney two sample test: n =60; W=696.5; P = 2.73e-04). As expected, abundance peaks in

November was not significantly different (Mann-Whitney two sample test: n =60; W= 531.5; P = 0.23). Biomass peaked earlier and was three times higher (November - 4.47g, Table 2.3.1) at Meletse than CoH WHS (January–2.98g, Table 2.3.1).

Table 2.3.4: Arthropod percentages (%) as reported by Botha *et al*. (2016) and the present study which were collected at sites belonging to Grassland and Savanna biomes. Collections by Botha *et al*. (2016) were undertaken during late mornings over a two months period whilst arthropods in the present study were collected at night.

	Grassland		**Savanna**	
	Botha *et al.* (2016)	**Present study**	**Botha *et al.* (2016)**	**Present study**
Acari	23.4	1	3.8	3
Araneae	9.5		8.5	
Coleoptera	5.5	19	2.7	29
Diptera	8.9	11	18.7	2
Hemiptera	25.9	19	32.3	7
Hymenoptera	14.9	5	16.1	37
Lepidoptera	0.06	42	3.5	19
Mantodea	0.06	0	0.7	0
Orthoptera	7.5	0	7.5	0
Thysanoptera	4.2	-	1.3	-
Unidentifiable	-	1	-	0
Isoptera (Infra Order)	-	0	-	3
Blattodea	-	1	-	0

My results differed from Botha *et al*. (2016) for both Grassland and Savanna samples. In addition, Botha *et al*. (2016) collected arthropods in the late mornings during the months of January and February to coincide with maximum biological activity. The present study sampled nocturnal arthropods. Although sampling was undertaken over a longer period, only two months of sampling from the present study (November and January) were used for comparison with Botha's *et al*. (2016) results as peak numbers were collected in these months. At the Grassland, arthropod proportions from my samples primarily consisted of Lepidoptera (42%) and lesser numbers of Arachnida (1%), Coleoptera (19%), Diptera (11%), Hemiptera (19%) and Hymenoptera (5%) (Table 2.3.4) whilst Botha *et al*. (2016) mostly found Acari (23.4%) and Hemiptera (25.9%) and lesser counts of Araneae (9.5%), Diptera (8.9%) and Hymenoptera (14.9%), as seen in Table 2.3.4. At the Savanna, samples from this study mostly consisted of Coleoptera (29%) and Hymenoptera

(37%) and lesser proportions of Arachnida (3%), Diptera (2%), Hemiptera (7%) and Lepidoptera (19%) (Table 2.3.4). Savanna arthropods collected by Botha *et al*. (2016), as seen in Table 2.3.4, mostly consisted of Hemiptera (32.3%) and lesser proportions of Araneae (8.5%), Diptera (18.7%), Hymenoptera (16.1%) and Orthoptera (7.5%).

2.4: Discussion

Savanna food resource availability across all study months: Arthropod abundance, biomass and order proportions across study months

My first hypothesis that temporal variations in arthropod availability within the dry and wet season reflects abundance and biomass is supported by my results as arthropod abundance and biomass was characterized by dry season lows and wet season peaks. This is consistent with Churchill (1994) where wet season samples represented 81.7% and 81% of the combined collected individuals and their biomass, respectively. Likewise, wet season arthropod samples in this study represented 68% of the combined abundance and 80% biomass. Pinheiro *et al*. (2002) also recorded peak arthropod abundance in the wet season although their research suggests that various taxa show different numeric responses relative to prevailing climatic conditions. Indeed, numeric response from this study were observed for Lepidoptera, which had the highest abundance in the dry season, whilst Coleoptera and Hemiptera showed moderate numbers at the same time. Conversely, Coleoptera and Hymenoptera had the highest abundance in the wet season. Other taxon, like infraorder Isoptera (order Blatodea), were only present in the wet season. In addition, arthropod size variation was greatest in the wet season as all size classes (size classes A, B, C, D, E, Table 2.3.2) were represented as opposed to the dry season when only the smaller sizes (A, B, Table 2.3.2) were represented. The many processes which contribute towards fluctuation in arthropod availability are not clearly understood (Pinheiro *et al*., 2002), with the variation in taxon richness and variation in size classes being most pronounced during wet season in the current study.

These temporal fluctuations in arthropod availability do have a cascading effect on higher trophic species which rely on them as a major food source (Churchill, 1994; Omogbeme & Oke, 2018; Rotenberry, 1980; Dinaw *et al*., 2017). Several studies of these arthropod predators have evidently shown that they align critical periods in their phenology such as breeding with maximal arthropod availability (Churchill, 1994; Omogbeme & Oke, 2018; Rotenberry, 1980; Dinaw *et al*., 2017). Findings from this study support this as bat activity recordings from the same area (Chapter 3: Table 3.3) showed corresponding peaks with arthropod availability.

Dry and wet season respective lows and highs in arthropod activity are due to the seasonal influence of precipitation and temperature (Barnett & Facey, 2016; Schowalter, 2011). Populations of terrestrial arthropod populations are sensitive to variations in water availability, temperature and plant availability (Barnett & Facey, 2016; Novais *et al*., 2016; Pinheiro *et al*., 2002; Schowalter, 2011). The arthropod integument constitutes of cuticle material which provides protection against water loss. Generally, the cuticle in larger arthropods is more sclerotized rendering the larger arthropods less sensitive to changes in water availability than smaller species (Barnett & Facey, 2016; Schowalter, 2011). Changes in rainfall affect plant productivity and quality thereby affecting the populations of herbivorous arthropods (Barnett & Facey, 2016; Walter *et al*., 2012). To deal with periods of low water availability and temperature, different arthropods employ different physiological and behavioral mechanisms such as entering a quiescent state or migrating (Schowalter, 2011). Within the wet season, arthropod availability decreased when precipitation reached a maximum in February (Table A.1a and Table 2.3.3). Pinheiro *et al*. (2002) suggested that stress factors caused by high precipitation and low food accessibility result in decreased arthropod numbers in the wet season. I therefore strongly suspect that arthropods had limited access to food resources in February when precipitation was highest which explains the recorded decrease in arthropod abundance.

Dry and wet season quantitative responses of two of the most abundant arthropod orders, Coleoptera and Lepidoptera

The most abundant order was Lepidoptera in the dry season, which made up 48% of arthropods collected during this period. All collected Lepidoptera characteristically rested their wings in a roof-like manner which, in most cases, is distinctive of the moth families in this order (Scholtz & Holm, 1985). Taxonomic verification of identificatied moth families was done using Scholtz & Holm (1985). Although the family level is not assessed as part of this thesis, it is worth mentioning that the micro Lepidoptera as well as the families Noctuidae and Geometridae (Scholtz & Holm, 1985; Smith, 2008) dominated captures in this period. These individuals were in their adult stages and were active in the dry months, indicating tolerance towards low water and temperature (Barnett & Facey, 2016; Berridge, 2012). Janzen (1987) listed some reasons as to why moths emerge in the dry season: (1) late emergence in the preceding wet season, (2) remaining, aging individuals, and (3) early emergence within the dry season due to either internal/external cue or environmental cues. Here, Lepidoptera abundance in the dry period gradually increased from June and peaked in

August and thereafter decreased till the onset of wet season (Table A.1a). During this study period, 2.8mm and 0.6mm of rainfall was observed in July and September, respectively (Table 2.3.3). These minute rainfall events are suspected to have cued individuals to emerge from pupa early and periodically. The third reason as proposed by Janzen (1987) better explains the observed trend as emerging adults are likely to have survived autumn and winter months. Janzen (1987) further made an example of a single generation of *Hemicephalis agenoria* (Noctuidae) pupae emerging at different times of the year, following rainfall, despite inhabiting the same tree host. Janzen (1987) also reported low recruitment as many species do not oviposit nor partake in mating during the dry season. There is little evidence to support reasons (1) and (2) in the present study as they both imply a gradual decrease in the population as the dry season progresses which was not observed here. Recruitment is generally very low in the dry season as few female moths will oviposit on host tree leaves. Other species of moth were not active during the dry season as reflected in the low diversity in sampled Lepidoptera. Such species likely succumbed to declining food resources as the nutritive content of plants reduced in the dry season (Walter *et al*., 2012). Despite any of the reasons which allowed for the survival of these Lepidoptera in the dry season conditions, their mere presence shows a resilience for low temperature and water availability. In addition, food availability is also ensured for the predators of these resilient Lepidoptera.

Coleoptera comprised 18% of sampled arthropods in the dry season. By observation, family diversity was lowest during this period with most individuals belonging to the Carabidae, Chrysomelidae and Scarabaiedae families (Davis *et al*., 2008; Scholtz & Holm, 1985; Smith, 2008). Furthermore, small sized individuals of less than 12.5mm in length were mostly collected (Table 2.3.2). The low rainfall and temperature conditions that are characteristic of the Savanna dry season (Du Toit & Cumming 1999; Rutherford *et al*., 2006b) result in diminished plant resource availability which is important for herbivorous arthropods (Scholtz & Holm, 1985; Schowalter, 2011; Barnett & Facey, 2016). Different species of Coleoptera employ various coping mechanisms to endure these abiotic conditions (Schowalter, 2011). Some species are known to suspend development of the active stage (known as diapause) to increase the potential of survival during unfavorable dry season conditions (Hodek, 2012). The initiation and thereafter termination of diapause is driven by photoperiod and exposure to threshold temperatures (Schowalter, 2011). For example, *Coccinella septemounctata* (family = Coccinelidae, Scholtz & Holm, 1985) enters an adult stage diapause during which no feeding takes place and ovary development ceases (Hodek, 2012).

The second hypothesis for this study was that arthropod availability varies across patches of vegetation which exhibit different levels of vegetation clutter. Arthropod availability did varyacross open, edge and closed vegetation clutter types. This occurred in terms of biomass than abundance as the proportion of arthropod numbers and size was temporally variable across vegetation clutter types. Limited number of studies to my knowledge, compare arthropod abundance and biomass between different levels of vegetation clutter. The results from the present study correspond with Botha *et al*. (2016) as higher abundance and biomass was found in closed vegetation clutter although this only stood in the dry season. Arthropod availability (abundance and biomass) was highest in the open vegetation during wet season. The temporal and spatial factors which influence arthropod availability at vegetation clutter level are not clearly understood at this level and more studies are needed in this regard.

Savanna vs CoH WHS: Savanna and Grassland food resource availability comparison

The results of this study show that CoH WHS (Grassland) had higher arthropod abundance and biomass for 2/3 months compared to Meletse. This is contrary to the third hypothesis which posits that the Savanna has greater arthropod availability than the Grassland due to a more complex vegetation structure. The exception was in November when biomass at Meletse (Savanna) was nearly four times higher than CoH WHS during which time a higher proportion of larger sized arthropods were collected. It is unclear as to whether my findings conform to Schadek *et al*. (2008) as species richness was not specifically tested at each study area. From a taxonomic and biomass point it does seem that Meletse provides a greater arthropod variety and availability. Indeed, Meletse had a greater number of arthropod families whilst the larger sized individuals, which contribute largely towards biomass, were also recorded in larger proportions. In addition, large scale emergence events were more frequent at Meletse especially for taxa such as sub-order Isoptera and Order Ephemeroptera in response to wet season condititions. The higher samples of these wet season emerging arthropods at Meletse might be an artefact of sampling bias as more days were spent at Meletse than CoH WHS.

Arthropod size proportions were, as aforementioned, considerably different between the two study areas. It is assumed that larger sized arthropods with greater biomass potentially have greater energy returns than their smaller counterparts for arthropod predators (Jenkins, 2015). However, prey size has been associated with taxa and hardness and both have been implicated as factors influence arthropod prey access to predator species (Aguirre *et al*., 2003; Freeman & Lemen, 2006). Aguirre *et al*. (2003) indicated that for Coleoptera, a larger size usually relates to a harder shell. The findings of Freeman & Lemen (2006) further suggested that softer prey cost less mechanical energy to chew than their harder shelled counterparts. It is hypothesized that predators target prey based on its size (Aguirre *et al*., 2003; Freeman & Lemen, 2006). However, further studies are required to better understand how the inter-relationships between arthropod size, hardness and taxa ultimately affect their selection as prey to predator species.

2.5: Conclusion

Temporal variations in arthropod availability at Meletse followed the predicted pattern of dry season lows and wet season highs. Interestingly, biomass quantity was better associated with the size of arthropods present rather than their abundance. This meant that peak periods in the wet season had greater proportions of larger arthropods which resulted in the higher biomass which was observed at the time. In addition, taxa variety increased from dry to wet season. The implications of this to predator species, is a more varied diet in terms of prey size and taxa during the wet season as opposed to the dry season. However, arthropod taxa including Hemiptera and Lepidoptera peaked in the dry season thereby potentially offering a food source during a food scarce period.

A common occurrence in both study areas is the presence of anthropogenic disturbance which, in literature terms, can be defined as land-use change (Birkhofer *et al*., 2015). The Meletse study area has been prospected for possible mining (Almond, 2012) to which Kearney & Seamark (2012) recommend that monitoring of bats should take place before, during and after blasting events to aid in decision making for mitigating impacts. Kearney and Seamark (2012) mentioned that development of roads, pits and processing areas resulting from mining would cause the loss of foraging and drinking habitats for bats. Land use practices such as infrastructural development and farming (wildlife and agricultural) were observed at both CoH WHS and Meletse along the peripherals which places these study areas on the edge of land-use change. Disturbances resulting from land-use practices can alter the functioning of ecological processes and therefore compromise ecosystems (Naeem *et al*., 1999). Such disturbance has been associated with biodiversity loss (Birkhofer *et al*., 2015).

Attributes of land-use change such as intensive habitat fragmentation, urbanization and agriculture can either stimulate or reduce available niche-space resulting in a positive or negative impact on affected species communities, including arthropod populations (Birkhofer *et al*., 2015). Future studies at both study areas and similar systems have to therefore consider land-use change impacts on wildlife.The results of the present study have shown that both areas have similarly high arthropod abundance which potentially makes them critical reservoirs of food resources to both obligate and non-obligate arthropod predators. Given that several species prey on arthropods as a main or partial food source, it is within reason to state that periods when arthropod availability peaked are critical for such predators especially those which have aligned their breeding times with maximum arthropod availability. An example of such a predator is the Minopterus *natalensis* such population which uses Meletse as a maternity roosting site in the wet season (van der Merwe, 1975). Furthermore, periods of low arthropod availability, associated with lower rainfall and temperatures, present greater challenges to arthropod predators in terms of food resources. Various methods are thus employed to avoid this period of low resource availability including migration, decreasing activity or foraging on alternative food items. Nonetheless, the availability of arthropods during the dry period at these areas (CoH WHS and Meletse) is an indication of potential food sources for resident predator species.

Findings from this study have demonstrated that natural habitats on the edge of land-use change can sustain diverse arthropod communities and thus maintain food resource reservoirs for various predator species. However, further changes in land-use which encroach into these areas will alter the vegetation structure which will have unknown effects on the diversity of arthropods and their food resource potential. Strict measures have to therefore be implemented to protect these and other similar areas. This includes keeping any anthropogenic activity in such areas minimal in order to protect the integrity of their ecosystems.

2.6: References

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Chapter 3: Relating bat activity and food resource availability at Meletse and Cradle of Humankind World Heritage Site

3.1: Introduction

Animals are subject to various ecological process which is reflected in their temporal activity patterns (Churchill, 1994). In order to survive in their environments, animals have to implement strategies which synchronize activity with the availability of critical resources such as food, temperature and water (Churchill, 1994). These resources fluctuate based on prevailing local climatic conditions in time. For example, rainfall and temperature increase in summer which stimulate productivity of vegetation and phytophagous orgasms. In contrast, temperature and rainfall decrease in winter which results in the decline or reduced activity of organisms which depend on them. For insectivorous bats, local climatic conditions have direct and indirect implications. Jones *et al*. (2009) suggested optimum ambient temperature as a direct influence stimulating bat activity. While, Burles *et al*. (2009) suggests that the influence of weather conditions on the activity patterns of ectothermic arthropod prey indirectly affects local food resource availability. Two of South Africa’s largest biomes, Savanna and Grassland, cover relatively 32.5% and 27.9% of the land area, respectively (Mucina & Rutherford, 2006). Local climatic conditions in both biomes are characterised by periods of temperature and precipitation lows (dry season) and highs (wet season) (Du Toit & Cumming 1999; Rutherford *et al*., 2006b). During the wet season, plant growth is stimulated by optimum temperatures and precipitation resulting in increases in arthropod abundance (Barnett and Facey, 2016; Schowalter, 2011). Dry season conditions bring about substantial decreases in the activity and abundance of several arthropods (Barnett and Facey, 2016; Berridge, 2012).

Mello *et al*. (2009) linked diet preference and the temporal availability of food resources to the timing of reproductive effort. Different bats have decreased activity during periods of low resource availability (dry season) and will enter into torpor and subsequently delay reproductive efforts (Burles *et al*., 2009; Jones *et al*., 2009). As primary predators of nocturnal flying arthropods, bats respond to changes in arthropod prey through their activity patterns (Jones *et al*., 2009). Female parturition and in some cases male spermatogenesis in bats is timed to periods of critical resource availablitity (Churchill, 1994; Jong, 1994; Taylor & O’Neil, 1988). Nonetheless, bats have been shown to time their activity patterns such that the most energy demanding time in their phenology coincides with times of increased food resources availability.

In addition to temporal limitations in arthropod availability, foraging bats must detect, classify and localize their prey which, depending on the amount of clutter in the background, poses a perceptual challenge to the bat (Schnitzler & Kalko, 2001). Different bat species have various echolocation and wing morphology adaptations to maneuver and hunt in different levels of clutter found in their habitat (Aldridge & Rautenbach, 1987; Norberg & Rayner, 1987; Schnitzler & Kalko, 2001, Schoeman & Jacobs, 2008). Echolocation systems are split into low-duty (LDC) and high-duty (HDC) cycle wherein emitted pulses and returning echoes are either separated in time (LDC) or frequency (HDC) (Fenton *et al*., 2012).These echolocation systems (LDC or HDC) are usually associated with different echolocation pulses as perceived by bat detectors (Monadjem *et al*., 2010). Echolocation pulses can either be frequency modulated (FM), quasi constant frequency (QCF) and constant frequency (CF) (Monadjem *et al*., 2010). To understand the foraging behaviour of bats in different levels of clutter, studies have investigated the association between echolocation calls and wing morphology (Aldridge & Rautenbach, 1987; Norberg & Rayner, 1987; Schnitzler & Kalko, 2001; Schoeman & Jacobs, 2008) and therefore categorized different bat species into foraging guilds (Table 3.1.1). Wing morphology factors in the wing loading (body mass/wing area), aspect ratio (square of wingspan/wing area) and wing tip index (Aldridge & Rautenbach, 1987; Norberg & Rayner, 1987; Schnitzler & Kalko, 2001; Schoeman & Jacobs, 2008). The combined characters of low wing loading and short wings correlate with slow, maneuvering flight which is suited for cluttered environments (Norberg & Rayner, 1987). Whilst high speed flight is associated with high wing loading which is suited for foraging in open areas (Norberg & Rayner, 1987).

Schnitzler and Kalko (2001) categorized bats into uncluttered space, background clutter space (edge) and highly cluttered space feeding guilds. Monadjem & Reside (2008) investigated the distribution and density of bats with different echolocation systems under the different levels of vegetation clutter and reported that bats discriminate between microhabitats as CF and FM bats selected for areas with high clutter whilst QCF avoided such areas. Few studies have investigated the temporal differences in the use of different levels of clutter by various bats, especially in relation to food resource availability. Insectivorous bats echolocate to maneuver between obstacles and locate potential prey items (Kalko & Schnitzler, 1989). During echolocation, call sequences can include search-phase (detection of prey items/navigation), approach-phase (pursuit of prey items) and feeding buzzes just before catching prey (Kalko & Schnitzler, 1989). Since the present study was only concerned with general bat species activity, only search –phase calls were assessed. Characteristics of search –phase calls including their repeated emission, species –specificity (unique to a species) and retention of call structure in a call sequence (O'Farrell *et al*., 1999) enable acoustic identification of bat species (Murray *et al*., 2001).

Table 3.1.1: Foraging guild based on wing morphology measurements derived from literature for bats reported in this study.

	Foraging guild	**Wing Loading (N/m^2)**	**Aspect ratio**	**References**
Minopterus natalensis	Clutter-edge	10.7	7.0	Norberg & Raynar (1987); Schoeman & Jacobs (2008); Schoeman & Jacobs (2003).
Rhinolophus blasii	Clutter	7.6	5.6	Schoeman & Jacobs (2008); Schoeman & Jacobs (2003).
Rhinolophus simulator	Clutter	5.4	6.7	Schoeman & Jacobs (2008); Schoeman & Jacobs (2003).
Neoromicia capensis	Open/Clutter-edge	7.1	6.4	Aldridge & Rautenbach (1987); Schoeman & Jacobs (2008)
Scotophilus dinganii	Open/Clutter-edge	12.4	7.3	Aldridge & Rautenbach (1987); Schoeman & Jacobs (2008)
Pipistrellus rusticus	Open/Clutter-edge	7.0	6.8	Aldridge & Rautenbach (1987); Schoeman & Jacobs (2008)
Myotis tricolor	Clutter-edge	7.5	5.6	Norberg & Raynar (1987); Schoeman & Jacobs (2008)
Tadarida aegyptiaca	Open	13.1	8.3	Schoeman & Jacobs (2008)
Taphozous mauritianus	Open	15.7	7.2	Schoeman & Jacobs (2008)

This study seeks to add knowledge on the temporal dynamics between bats and their arthropod prey. Changes in the temporal activity patterns of bats and arthropods were therefore investigated. Two areas within karst landscapes of a Savanna and Grassland system were of interest. Karst landscapes comprise of carbonate bedrock (limestone, dolomite or chalk) and through the excavating effect of water, dissolve over time to form caves, underground rivers and springs (Belo, 2003). Clement *et al*. (2006) and Struebig *et al*. (2009) reported on the importance of karst landscapes in providing roosting space for cave-roosting species. Both Savanna and Grassland areas are diverse in bat species (ACR, 2018; Kearney *et al*., 2017) although very little has been reported on their temporal patterns. I also investigate the foraging guilds of bats in respect to temporal (dry season to wet season) differences in activity patterns (open, edge and closed vegetation clutter). I therefore (1) hypothesize that temporal bat activity patterns coincide with arthropod availability. Given that arthropod activity is expected to peak in the wet season at both the Savanna and Grassland, (2) bat activity will peak in response to increased arthropod availability and abundance. Temporal bat activity and arthropod availability will also (3) vary across different levels of vegetation clutter at the Savanna.

3.2: Methods

Study Areas

Sampling occurred at two South African karst landscapes of different biomes. Bat assemblages from both study areas include cave roosting and non-cave roosting species. Meletse, Limpopo Province, represented the Savanna. Known roosting caves include Madimatle Cave (also known as Gatkop Cave), 24°37’S 27°40’E (Kearney *et al*., 2017). Grassland sampling was located in the Cradle Nature Reserve (25. 91957 S 027.83521 E) within the CoH WHS, Gauteng Province. Visual observation indicated agricultural activity and infrastructural development to various extents in local and broader areas of sites in both study areas. See chapter 2 for detailed description of the vegetation and climatic regimes of the Savanna and Grassland biomes.

Echolocation data collection

Anabat SD2 (Titley Electronics, Ballina, NSW) bat detectors were used to record and save echolocation bat calls. The internal clock of each detector was synced to a single computer which would later be used for analysis. Both time zone settings on the computer and the CFRead (Chris Corben, version 4.4n, 2011) software were set to UTC+02:00 whilst the clock was aligned with GPS time (www.time.is.com). The CF cards for storing data on the AnaBAT SD2 were initialized on CFRead to change the storage format into DAT which allowed for echolocation call data to be downloaded for analysis. Recording of bat activity was set 30min before sunset and 30min after sunrise.

Deployed bat detectors were placed in waterproof casings which had a PVC elbow opening for the microphone (Figure 3.2.1). Sprong *et al*. (2012) reported that the microphone range on an Anabat SD2 is limited to 5m on the PVC elbow waterproofing casing. In the same study, the same SD2 had a higher range of 15m when deployed without a PVC water proofing case. The range limitation applied by the PVC elbow was therefore expected. Power for each bat detector was sourced from a 12V 2.4AmpHour batteries which allowed for longer usage at lower costs as opposed to standard 1.5V AA batteries. To protect the bat detector in case of current overload, a 250mAmp fuse was fitted to the wiring to interrupt flow. The ensemble of bat detector, battery and wiring was placed inside a sealable case (Figure 3.2.1). The inside of the case was lined with pieces of polystyrene for insulation and naphthalene marbles were placed inside to repel insects during deployment

(Figure 3.2.1a). A 30cm length of hoop iron was bent and bolted to the underside to hook the case onto a tree whilst plastic cable tie was used to re-enforce the mounting (Figure 3.2.1b &d).

Each month (sampling event), bat detectors were deployed in open, edge and closed vegetation clutter types where they were mounted onto a tree as shown in Figure 3.2.1. Descriptions of vegetation clutter types is outlined in Chapter 2 (2.2 Methods). Bat echolocation calls were recorded for nine consecutive months (June 2017 to February 2018) at the Meletse study area (Savanna) and three non-consecutive months (September 2017, November 2017 and January 2018) at CoH WHS study area (Grassland). Three bat detectors were deployed at Meletse for ten nights to achieve a sample size of 30 per sampling event. To standardize the number of samples, sampling effort was matched at CoH WHS by utilizing five bat detectors for six nights. Within each study area, sampling effort differed each month due to temporal variation in sunset and sunrise times. The planned number of nights (Meletse = 10 nights and CoH WHS = 6 nights) were expected to yield set values of duration effort which was calculated in hours (Table 3.3.2). However, instances of data loss resulted in ‘actual’ duration effort being lower than ‘planned’ duration effort for August, October, December, January and February (Table 3.3.2). Duration effort was based on the number of hours a bat detector was recording. In order to confirm this, data logs from each recording session were used to corroborate the recording of bat activity. In some instances, there were nights with missing data and associated logs to state whether the bat detector switched on or not and such nights were considered as errors and ruled out. Conversely, data loss (lost duration effort) was considered for nights with no acoustic activity but have associated logs verifying that the bat detector did record. Duration of each sampling event was corrected for the start (30min before sunset) to the end (30min after sunrise) of recording. Recorded echolocation data from each sampling event was downloaded and saved into the computer for later analysis.

Recording success was calculated using log data evidence. The number of hours that the bat detector recorded (actual duration effort) was divided by the standardized planned number of hours and the resulting value was subtracted from a hundred percent to give the success. An anti-noise filter was used to clean out undesired noises and ultimately determine combined bat activity. The filter has a characteristic frequency (Fc) range of 5–200 kHz, smoothness factor 50, which cleans out most non-bat noises from call files. As the name implies, the anti-noise filter was used to

Figure 3.2.1: (a) Waterproof case with Anabat SD2, wiring with 250mAmp fuse and 12V, 2.4AmpHour battery inside. The waterproof case was (b) mounted onto a tree using (d) hoop iron attached beneath. Each case had a (c) PVC elbow opening for the microphone.

identify combined bat acoustic activity. At species level, bats show greater variation in call characteristics (Monadjem *et al*., 2017). As practiced in several bat acoustic studies, calls are collected and their characteristics are used to create a bat echolocation call library which allows one to acoustically discriminate different species' calls (Linden *et al*., 2014; Monadjem *et al*., 2017). Release calls of bats occurring at the Meletse and CoH WHS study areas were therefore recorded to establish a call library of local species (also see Linden *et al*., 2014; Monadjem *et al*., 2017; Taylor *et al*., 2013).

Calls were recorded on the Anabat SD2, which is zero-crossing, and were subsequently analyzed using AnaLookW (Chris Corben, version 0.4.2.7, 2016). Call data from each month and respective vegetation clutter type was scanned using specific filters in AnaLookW, using each created filter, to extract the total number of bat passes (files) and calls in one-minute time blocks. This partitioning of echolocation data is referred to as the Acoustic Activity Index (AAI) (Abel, 2011; Miller, 2001). The AAI is based on presence/absence of bat acoustic activity within a given duration of acoustic surveying. To better present changes in bat activity and differences between species, Miller (2001) split the acoustic survey into 1min time blocks. Files containing bat recordings are given a score of 'one' irrespective of the number of identifiable call sequences/pulses for a given species (Miller, 2001). After running scans on AnaLookW, filtered text files (consisting of number of bat files and calls in 1min time blocks) were sorted into respective months (June to February) and vegetation clutter types (open, edge and closed) and subsequently imported into excel sheets. To standardize species comparison, AAI for each species was obtained by dividing bat passes by the unit time effort for each respective month and expressed as a percentage (Miller, 2001). The formulae AAI = bat passes/time effort *100 was therefore used. In addition, the number of hours from midnight (00:00) to the time when the bat detector was programmed to switch off, was subtracted to standardize the sampling duration effort of each sampling event.

Arthropod abundance and biomass data collection

Monthly arthropods data collections (see Chapter 2, 2.2 Methods) were compared with bat activity. The monthly arthropod capture success (CS) (Chapter 2, Table A.1a) and biomass (Chapter 2, Table 2.3.1) of collected arthropods were sorted according to open, edge, closed vegetation clutter types as well as combined samples. Aldridge & Rautenbach (1987) categorized arthropods into large, medium and small size classes. In the present study, arthropods were also grouped by size although stricter measurements were used to discriminate between each size class. The abundance and biomass proportion of collected arthropods were therefore categorized into size classes A-E (Table 2.3.2). The length and width of each size class were as follows: A (<4.5mm×2.6mm), B (<12.5mm×3.5mm), C (<17.8mm×5.7mm), D (18.1mm×9.5mm) and E (30.3mm×6.4mm).

Data Analysis

A Spearman's test was run to determine the degree of correlation between temporal bat activity and arthropod availability (Chapter 2) from the Meletse study area for combined and open, edge and closed vegetation clutter types. Temporal variation in bat activity and arthropod availability

(Chapter 2, 2.2 Methods) were tested across sampled months at Meletse (June 2018–February 2018) using a Kruskal–Wallis one-way analysis of variance test, and a Wilcox two sample test for subsequent months at CoH WHS (September and November, 2017, and January 2018). A *post hoc* Dunn test (version 1.3.2, Dinno, 2016) was further performed for the Meletse data to obtain pair-wise comparisons (Z stats and P value) of bat activity and arthropod availability (Chapter 2, 2.2 Methods) between sampled months. Temporal variations in bat activity and arthropod availability were also compared across different vegetation clutter types (open, edge and closed) using Kruskal–Wallis one-way analysis of variance test followed by *post hoc* Dunn test (package dunn.test version 1.3.2, Dinno, 2016). All statistics were ran on R version 3.1.2 (R Core Team, 2014) with scripts developed from the programs RStudio version 1.1.423 (RStudio, 2018) and R Commander version 2.1.7 (Fox, 2005).

3.3: Results

Meletse temporal bat activity and food resource availability

Acoustic survey effort at Meletse for different vegetation clutter were as follow: open (972.5hrs), edge (883hrs) and closed (749hrs). Data from some nights is omitted (Table 3.3.2) and this can be attributed to instances of lost data due to CF card malfunction after recording (Table 3.3.2). Combined bat activity was lowest in June (AAI = 0.55%, Table 3.3.4) and highest in November (AAI = 46.99%, Table 3.3.4). Shapiro–Wilk test revealed non- normality ($p < 0.01$) for all the bat activity data, hence non–parametric statistical tests were performed. Bat relative activity was significantly different between months (Kruskal-Wallis ANOVA: $\chi 2 = 150.46$, d.f = 8, $P < 0.01$). From June to November, a continuous monthly increase in AAI was observed (Table 3.3.4). Throughout the dry season months, AAI increased significantly (compared to the previous month) in August (*Z. stat* = 1.77, $P < 0.04$, Table 3.3.1) and September (*Z. stat* = -3.30, $P < 0.01$, Table 3.3.1). In the subsequent wet season, a peak in AAI occurred in November (*Z. stat* = 3.34, $P < 0.01$, Table 3.3.1) followed by non-significant decreases in December (*Z. stat* = 0.44, P = 0.33, Table 3.3.1) and January (*Z. stat* = 0.78, P = 0.22, Table 3.3.1) and a significant drop in February (*Z. stat* = -1.71, P = 0.04, Table 3.3.1).

Table 3.3.1: Pairwise comparisons for monthly bat activity between all the sampled months at Meletse (Savanna). The Z-statistic and P-value (parenthesis) are reported.

	June	**July**	**August**	**September**	**October**	**November**	**December**	**January**
July	-0.425685 (0.3352)							
August	2.384799 (**0.0085**)	1.77496 (**0.038**)						
September	-5.562293 (**0**)	4.724282 (**0**)	-3.297441 (**0.0005**)					
October	-5.384757 (**0**)	4.63903 (**0**)	-3.280732 (0.0005)	0.247527 (0.4023)				
November	-9.320292 (**0**)	8.212422 (**0**)	-7.1973 (**0**)	3.899859 (**0**)	3.339821 (**0.0004**)			
December	3.841573 (**0.0001**)		-2.985016 (0.0014)	1.819194 (**0.0344**)	1.704792 (**0.0441**)	0.440385 (0.3298)		
January	-6.879846 (**0**)	6.160104 (**0**)	-5.033363 (**0**)	-2.341013 (**0.0096**)	-2.003357 (**0.0226**)	0.843208 (0.1996)	0.781455 (0.2173)	
February	-5.721953 (**0**)	4.95519 (**0**)	-3.628729 (**0.0001**)	-0.595524 (0.2757)	-0.323967 (0.373)	2.991824 (**0.0014**)	1.572533 (0.0579)	-1.711641 (**0.0435**)

P value < 0.05

Table 3.3.2: Echolocation sampling duration loss and success per vegetation clutter type (open, edge and closed) for Meletse (June 2017–February 2018) and CoH WHS (September, November, 2017, and January 2018). Each month, three bat detectors (B1, B2, B3) were deployed at Meletse whilst five detectors (B4, B5, B6, B7, B8) were deployed at COH WHS. Actual duration after loss (planned duration effort minus lost duration effort) was used to calculate recording success percentage (Actual/Planned *100).

	Vegetation clutter type	**Deployed bat detector**	**Planned duration (hours)**	***Lost duration effort (hours)**	**Actual duration after loss (hours)**	**Success (%)**
Meletse						
	Open	B1	145	0	145	100
June	Edge	B2	145	0	145	100
	Closed	B3	145	0	145	100
	Open	B1	145	0	145	100
July	Edge	B2	145	145	0	0
	Closed	B3	145	0	145	100
	Open	B1	135	0	135	100
August	Edge	B2	135	0	135	100
	Closed	B3	135	0	135	100
	Open	B1	130	0	130	100
September	Edge	B2	130	0	130	100
	Closed	B3	130	0	130	100
	Open	B1	120	0	120	100
October	Edge	B2	120	0	120	100
	Closed	B3	120	96	24	20
	Open	B1	120	0	120	100
November	Edge	B2	120	0	120	100
	Closed	B3	120	0	120	100
	Open	B1	110	110	0	0
December	Edge	B2	110	88	22	20
	Closed	B3	110	110	0	0
	Open	B1	115	57.5	57.5	0
January	Edge	B2	115	0	115	100
	Closed	B3	115	115	0	0
	Open	B1	120	0	120	100
February	Edge	B2	120	24	96	80
	Closed	B3	120	60	60	50

	Vegetation clutter type	**Deployed bat detector**	**Planned duration (hours)**	***Lost duration effort (hours)**	**Actual duration after loss (hours)**	**Success (%)**
Total			3420	805.5	2614.5	76
CoH WHS						
September	Open1	B1	81	0	81	100
	Open2	B2	81	0	81	100
	Open3	B3	81	0	81	100
	Edge	B4	81	0	81	100
	Closed	B5	81	0	81	100
November	Open	B1	72	0	72	100
	Edge1	B2	72	48	24	33
	Edge2	B3	72	0	72	100
	Edge3	B4	72	12	60	83
	Closed	B5	72	72	0	0
January	Open	B1	69	0	69	100
	Edge	B2	69	0	69	100
	Closed1	B3	69	0	69	100
	Closed2	B4	69	0	69	100
	Closed3	B5	69	0	69	100
Total			1110	132	978	88

*Event/night considered as loss when data is missing and there is no data log evidence of bat detector recording at the time

Species were disntinguished using call parameters (Fc, Tk, Fmin, Fmax and Duration) obtained from recorded individuals (Table 3.3.3). It is noteworthy that cited literature (Linden *et al*., 2014; Monadjem *et al*., 2017; Taylor *et al*., 2013) also used AnaLookW (Chris Corben, version 0.4.2.7, 2016) to analyze Anabat files. Albeit different versions of the software, these authors reported on Fc (characteristic frequency) as defined in AnaLookW. However, other studies have interchangeably used Fc with Fk (frequency at the knee) despite the latter having more variation. The present study reports on Fc as reported in other studies and not Fk. Release calls were recorded for 9 of the 13 species reported to occur at the Meletse study area (Kearney *et al*., 2017) including *Miniopterus natalensis*, *Neoromicia capensis*, *Pipistrellus rusticus*, *Rhinolophus blasii*, *Rhinolophus simulator*, *Rhinolophus smithersi* and *Scotophilus dinganii*. The two species *Neo. capensis* and *Sco. dinganii* overlapped in call frequencies (Fc = 40 kHz ± 5 kHz, Fmin=37.5 kHz

± 2.5 kHz, Fmax = 66.5 kHz ± 8.5 kHz and Dur = < 3.5 ms) which we considered as uniform enough to treat as one phonic group (35–45 kHz). Even though *P. rusticus* presents unique call characteristics, various calls with similar characteristics albeit broader Fc, Fmin, Fmax, and Dur were identified, and I therefore created a phonic group (44–49 kHz) to include *P. rusticus* and *Neo. zuluensis*. The 14–20 kHz, 20–27 kHz phonic groups were also scanned as they were present in the study area and detected by the Anti-noise filter. For the CoH WHS study area, release calls were obtained for *Neo. capensis*, *R. clivosus*, and *R. simulator* and thereafter used as reference calls to create filters for these species. Species known to occur at Meletse which did not have their release calls taken in the current study include *Cloeotis percivali*, *Hipposideros caffer*, *Myotis tricolor*, *Nycteris thebaica*, *Neoromicia zuluensis*, *Tadarida aegyptiaca*, *Taphozous mauritianus* (Chege *et al*., 2015; Kearney *et al*., 2017). For CoH WHS, I did not have release calls for the following species *Miniopterus fraterculus*, *Min. natalensis*, *Mops condylurus*, *Myo. tricolor*, Nyc. *thebaica, R. blasii, R.* darlingi, *Sauromys petrophilus, Sco. dinganii*.

Recorded activity at species/phonic group level (see Table 3.3.4 for detail) was highest for *Min. natalensis* (November–42.46%, Table 3.3.4) during the wet season and accounted for most of the bat activity during the November–January period (Table 3.3.4). Wet season peaks in AAI were also observed for the 20–27 kHz phonic group (February–2.64%, Table 3.3.4), *R. simulator* (November–2.5%, Table 3.3.4), *R. blasii* (November–0.58%, Table 3.3.4), 14–20 kHz phonic group (January–0.43%, Table 3.3.4), *R. smithersi* (October–0.21%, Table 3.3.4) and *R. clivosus* (December–0.18%, Table 3.3.4). Peaks for the 35 kHz–45 kHz (1.3%) and 44 kHz–49hHz (0.52%) phonic groups were observed in September (late dry season), as seen in Table 3.3.4.

Bat activity comparison between vegetation clutter types at Meletse

The highest relative activity was recorded at the edge and the lowest at closed clutter vegetation (Table3.3.4, Figure 3.3.1). High edge activity was apparent for all species and phonic groups (Table 3.3.4). In November, the peak month of activity, *Min. natalensis* presented an AAI of 23.12%, the highest recorded for a single species. *Miniopterus natalensis* activity in the open and closed vegetation clutter types was higher at 10.96% and 8.38% (Table 3.3.4, Figure 3.3.2a), respectively, compared to *R. simulator* (open = 0.29%, edge = 1.87%, closed = 0.35%, Table 3.3.4, Figure 3.3.2b) and *R. blasii* (open = 0.03%, edge = 0.46%, closed = 0.09%, Table 3.3.4, Figure 3.3.2c). *Rhinolophus smithersi* presented an activity peak earlier during the start of the wet season

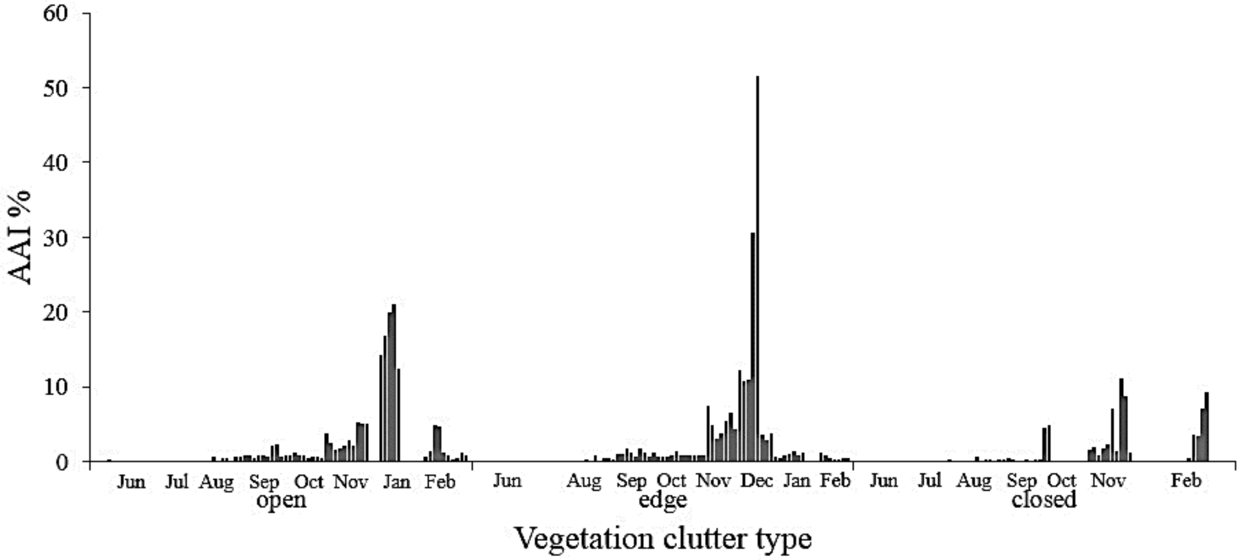

Figure 3.3.1: Combined nightly AAI % from June 2017–February 2018 across open, edge and closed vegetation clutter types at the Meletse study area, Limpopo Province.

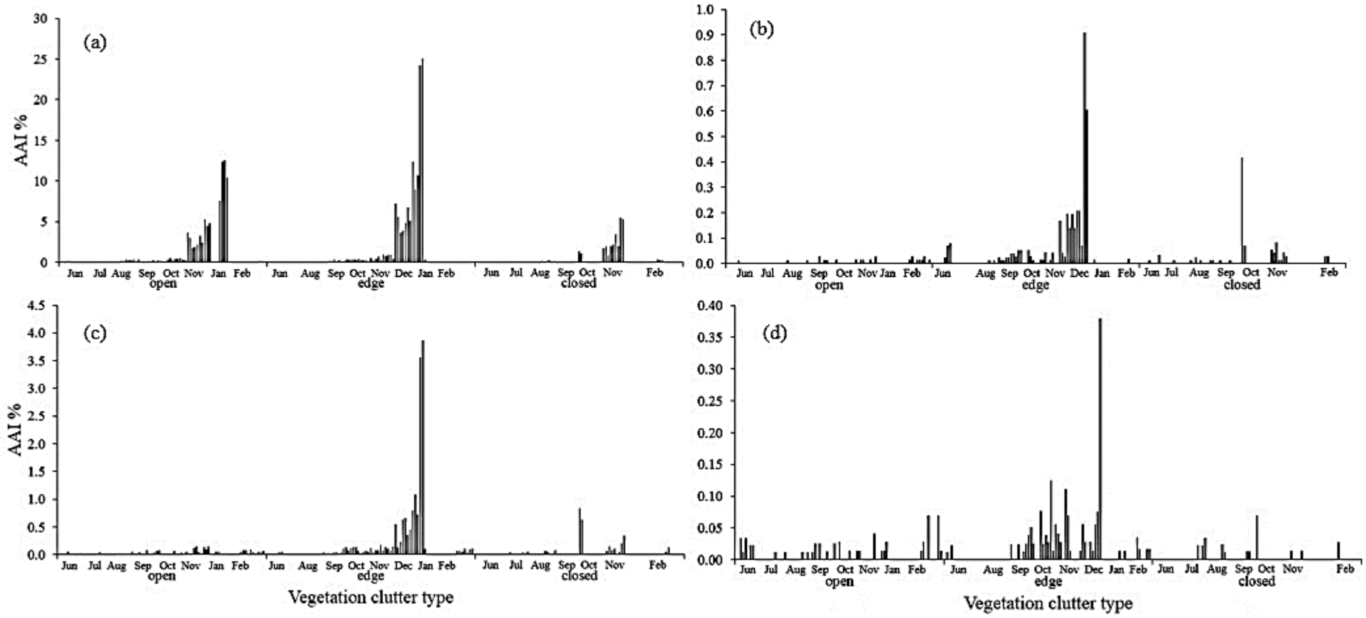

Figure 3.3.2: Nightly AAI% from June 2017 to February 2018 at open, edge and closed vegetation clutter types for (a) *Miniopterus natalensis*, (b) *Rhinolophus blasii*, (c) *Rhinolophus simulator* and (d) *Rhinolophus smithersi* for Meletse area.

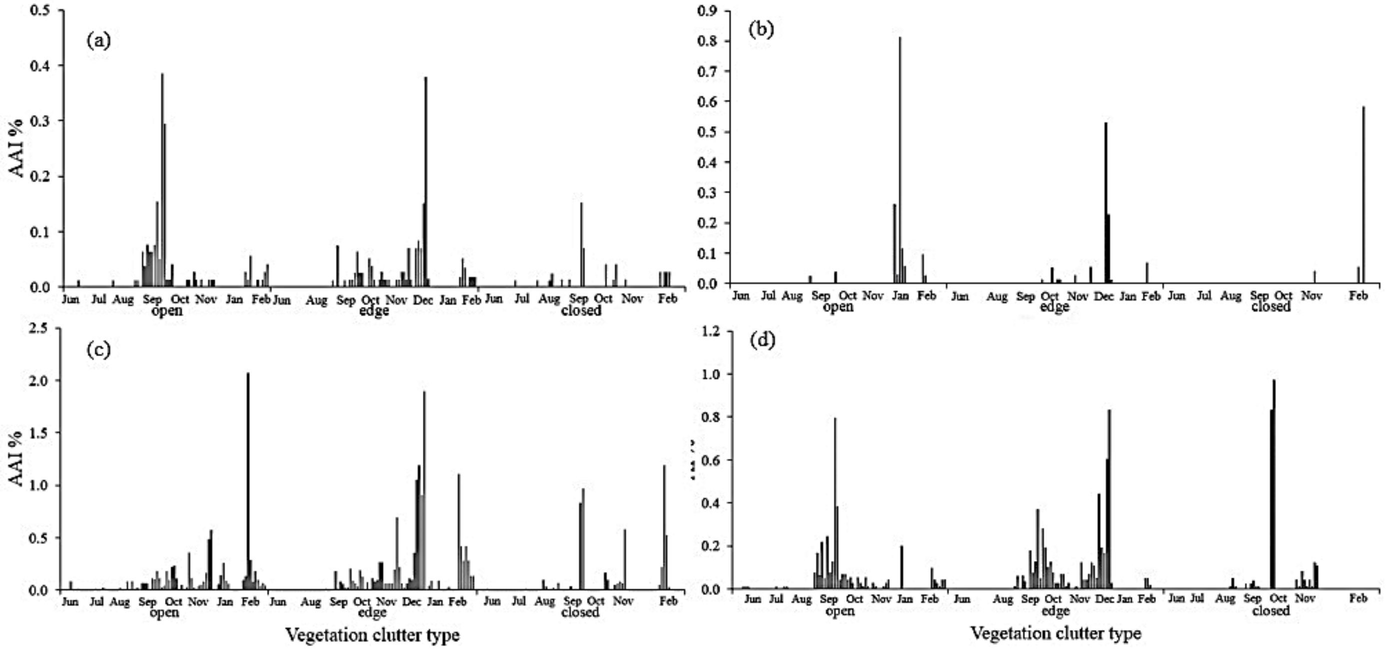

Figure 3.3.3: Nightly AAI% from June 2017 to February 2018 at open, edge and closed vegetation clutter types for (a) 44–49 kHz *(P. rusticus*), (b) 14–20 kHz, (c) 20-27 kHz and (d) 35–45 KHz phonic groups obtained at Meletse.

Table 3.3.3: Call parameters set for each filter using AnaLookW. Filters include Anti-noise, *Min. natalensis*, *R. blasii*, *R. simulator*, *R. smithersi*, 14–20k Hz, 20 - 27 kHz, 35–45 kHz (*Neoromicia capensis*/*Scotophilus dinganii*) and 44–49 kHz (*Pipistrellus rusticus*) phonic groups.

Species/Phonic group	**Number of individuals**	**Smoothness**	**Start (High/Low), all Drop**	**Maximum Change(+ve)**	**Maximum Change(-ve)**	**Fc(kHz) Min**	**Fc(kHz) Max**	**Fc (kHz) Mean**	**Tk(ms) Min**	**Tk(ms) Max**	**Fmin(kHz) Min**	**Fmin(kHz) Max**	**Fmax(kHz) Min**	**Fmax(kHz) Max**	**Dur(ms) Min**	**Dur(ms) Max**	**Recorded in current study?**	**Overlap species (unrecorded)**
Anti-noise		50	-	-	-	-	200		-	-	-	-	-	-	3	70		
Minopterus natalensis	6	30	-	-	-	51.8	57.95	54.88	-	-	-	-	-	-	0	70	Yes	
Rhinolophus blasii	4	35	High	-	-	85.22	88.89	87.06	-	-	-	-	-	-	-	-	Yes	
Rhinolophus clivosus	0	35	High	-	-	89.85	91.95	90.9	-	-	-	-	-	-	-	-	Yes	
Rhinolophus simulator	23	35	High	-	-	81.1	84.88	82.99	-	-	-	-	-	-	-	-	Yes	
Rhinolophus smithersi 47kHz	1	30	High	-	-	45.99	46.88	46.44	-	-	-	-	-	-	7.07	61.61	Yes	
Rhinolophus smithersi 44kHz	1	35	High	-	-	42.5	44.5	43.5	-	-	-	-	-	-	6.5	50	Yes	
14–20 kHz		35	High			14	19.95	16.98							2	14	No	*Chaerephon ansorgei* or *Mops midas* (O2; O4)
20–27 kHz		35	High			20	27	23.5							2.8	12	No	*Chaerephon pumilus* or *Mops* condylurus (O2; O3) *Tadarida Aegyptiaca* (O2; O4) *Taphozous mauritianus* (O1; O3; O4)
35–45 kHz (*Neoromicia capensis*/*Scotophilus dinganii*)		35	High	-	-	35	45	40	-	-	35	40	58	75	0.5	4	Yes	*Myotis tricolor* (O3; O4)
44–49 kHz (Pipistrellus *rusticus*/)		35	High	1	-	44	49	46.5	0	3	44	52	61	65	0.5	4	Yes	*Neoromicia zuluensis* (O2; O3; O4) and possibly *Myotis tricolor* (O4)

Key for overlap species references: O1: Fenton & Bell, 1981; O2: Linden *et al*., 2014; O3: Monadjem *et al*., 2017; O4: Taylor *et al*., 2013

Table 3.3.4: Acoustic activity index (%) for each filtered species/phonic group from the Meletse study area (Savanna) sorted according to vegetation clutter type (open, edge and closed) and combined pooled data (values are rounded-off to two decimal points) for the months of June 2017 to February 2018.

	Vegetation clutter type	**June**	**July**	**August**	**September**	**October**	**November**	**December**	**January**	**February**
All Bat	**Combined**	**0.55**	**0.51**	**2.77**	**8.46**	**8.72**	**46.99**	**27.40**	**33.83**	**15.10**
	Open	0.45	0.21	0.92	3.55	2.59	10.86	0.00	28.13	5.64
	Edge	0.05	0.00	1.16	3.93	2.96	23.31	27.40	5.70	1.53
	Closed	0.05	0.30	0.68	0.98	3.17	12.82	0.00	0.00	7.93
Miniopterus natalensis	**Combined**	**0.22**	**0.22**	**1.35**	**1.95**	**4.15**	**42.46**	**16.40**	**14.50**	**0.54**
	Open	0.16	0.12	0.57	0.60	1.19	10.96	0.00	14.33	0.22
	Edge	0.05	0.00	0.52	1.06	2.13	23.12	16.40	0.17	0.01
	Closed	0.01	0.10	0.26	0.30	0.83	8.38	0.00	0.00	0.31
Rhinolophus blasii	**Combined**	**0.08**	**0.01**	**0.07**	**0.13**	**0.21**	**0.58**	**0.50**	**0.00**	**0.07**
	Open	0.00	0.00	0.00	0.02	0.00	0.03	0.00	0.00	0.04
	Edge	0.06	0.00	0.04	0.10	0.04	0.46	0.50	0.00	0.01
	Closed	0.02	0.01	0.02	0.01	0.16	0.09	0.00	0.00	0.02
Rhinolophus clivosus	**Combined**	**0.04**	**0.00**	**0.00**	**0.01**	**0.05**	**0.14**	**0.18**	**0.00**	**0.00**
	Open	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Edge	0.04	0.00	0.00	0.00	0.00	0.13	0.18	0.00	0.00
	Closed	0.00	0.00	0.00	0.00	0.05	0.01	0.00	0.00	0.00
Rhinolophus simulator	**Combined**	**0.11**	**0.08**	**0.25**	**0.47**	**0.92**	**2.50**	**2.47**	**0.10**	**0.44**
	Open	0.05	0.02	0.08	0.12	0.08	0.29	0.00	0.03	0.18
	Edge	0.03	0.00	0.12	0.29	0.36	1.87	2.47	0.07	0.17
	Closed	0.02	0.07	0.05	0.06	0.49	0.35	0.00	0.00	0.08
Rhinolophus smithersi	**Combined**	**0.05**	**0.03**	**0.04**	**0.14**	**0.21**	**0.11**	**0.17**	**0.00**	**0.10**
	Open	0.04	0.01	0.01	0.03	0.02	0.03	0.00	0.00	0.06
	Edge	0.01	0.00	0.02	0.10	0.16	0.06	0.17	0.00	0.03
	Closed	0.00	0.03	0.01	0.01	0.02	0.01	0.00	0.00	0.01
14–20 kHz	**Combined**	**0.00**	**0.00**	**0.01**	**0.03**	**0.02**	**0.03**	**0.25**	**0.43**	**0.28**
	Open	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.43	0.04
	Edge	0.00	0.00	0.00	0.02	0.02	0.02	0.25	0.00	0.02
	Closed	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.21
20–27 kHz	**Combined**	**0.03**	**0.02**	**0.27**	**0.58**	**1.36**	**2.32**	**0.93**	**0.29**	**2.64**
	Open	0.03	0.02	0.08	0.25	0.32	0.64	0.00	0.20	1.04
	Edge	0.00	0.00	0.13	0.28	0.43	1.30	0.93	0.08	0.93
	Closed	0.00	0.00	0.06	0.05	0.60	0.38	0.00	0.00	0.68
35–45 kHz	**Combined**	**0.01**	**0.01**	**0.08**	**1.30**	**0.82**	**0.69**	**0.47**	**0.07**	**0.13**
	Open	0.01	0.01	0.00	0.74	0.13	0.06	0.00	0.07	0.09

	Vegetation clutter type	**June**	**July**	**August**	**September**	**October**	**November**	**December**	**January**	**February**
	Edge	0.00	0.00	0.06	0.53	0.08	0.46	0.47	0.00	0.04
	Closed	0.00	0.00	0.02	0.04	0.60	0.16	0.00	0.00	0.00
44–49 kHz	**Combined**	**0.00**	**0.01**	**0.06**	**0.52**	**0.14**	**0.20**	**0.17**	**0.00**	**0.15**
	Open	0.00	0.00	0.01	0.42	0.03	0.03	0.00	0.00	0.06
	Edge	0.00	0.00	0.03	0.09	0.04	0.13	0.17	0.00	0.05
	Closed	0.00	0.00	0.02	0.01	0.07	0.04	0.00	0.00	0.04

in October (open =0.02%, edge = 0.16%, closed = 0.02%, Table 3.3.4, Figure 3.3.2d), with the edge vegetation structure detectors presenting highest activity of the three vegetation clutter types. A similar pattern was found across all the other Rhinolophid species at the study area.

The 14–20 kHz phonic group showed the lowest activity compared to other phonic groups. A peak of 0.43%, primarily in the open vegetation (AAI = 0.43%), was recorded for the 14–20 kHz phonic group in January (Table 3.3.4, Figure 3.3.3b). The Verspertilionids belonging to the phonic groups 35 kHz–45 kHz (*Neo. capensis* /*Sco. dinganii*) and 44 kHz–49 kHz (*P. rusticus*/*Neo. zuluensis*) exhibited peaks in September. Peaking at 0.52% (open = 0.42%, edge = 0.09%, closed = 0.01%, Table 3.3.4, Figure 3.3.3a), the low activity exhibited by the 44 kHz–49 kHz phonic group was similar to that of the 14–20 kHz phonic group. A more intermediate activity peak was presented by the 35 kHz–45 kHz phonic group at 1.30% (open = 0.74%, edge = 0.53%, closed = 0.04%, Table 3.3.4, Figure 3.3.3d). Activity gradually decreased for both Verspertilionids groups from the peak month (September) to February (Table 3.3.4). An activity increase was recorded in the 20-27 kHz phonic group later in the wet season (February) with a peak of 2.64% (open = 1.04%, edge = 0.93%, closed = 0.68%, Table 3.3.4, Figure 3.3.3c). Similar activity of 2.32% (Table 3.3.4) was exhibited in the early wet season (November) for the 20-27 kHz phonic group, although this was higher at the edge vegetation (open = 0.64%, edge = 1.30%, closed = 0.38%, Table 3.3.4, Figure 3.3.3c). The majority of acoustic activity recorded in January (AAI = 33.83%, Table 3.3.4) and February (AAI = 15.10%, Table 3.3.4) could not be accounted for at species level.

A total of 3418 individual arthropods were collected (outlined in Chapter 2, 2.3 Results) in conjunction with echolocation data collection spanning dry to wet season months (June to February). Arthropod abundance was lowest in June (Chapter 2, Table A.1a). A gradual increase was thereafter seen in the months that followed peaking significantly in August (Chapter 2, Table

A.1a and Table A.2a). In the wet season, a significant rise and all-time peak occurred in November (Chapter 2, Table A.1a and Table A.2a) and gradually decreased until February. The arthropod orders Coleoptera, Diptera, Hemiptera, Hymenoptera and Lepidoptera were the most represented out of the 15 collected taxa (Table A.1a).

Arthropod captures did, however, differ temporally for each order. During June to September (dry season), captures primarily consisted of Coleoptera, Hemiptera and Lepidoptera. Initially, in the first sampling event (June), combined CS for Coleoptera, Hemiptera and Lepidoptera were 0.025, 0.003 and 0.024 ind./trap-hours, respectively. In the following months between July and September, an increasing trend was observed for Hemiptera and Lepidoptera, reaching respective combined CS of 0.039 and 0.072 ind./trap-hours (Table A.1a). Meanwhile, Coleoptera captures decreased to combined CS as low as 0.013 ind./trap-hours during the same period. Arthropod abundance was largely consisted of size class A (<4.5mm×2.6mm) arthropods which always comprised more than 66% of captures (Table 2.3.2). The biomass of larger size classes B (<12.5mm×3.5mm) and C (<17.8mm×5.7mm) arthropods did, however, make up higher counts reaching respective highs of 56% and 70% (Table 2.3.2). In November (wet period), when the greatest number of arthropods were collected, major emergence events were seen for Coleoptera, Hymenoptera and Lepidoptera (Table A.1a) but captures later stabilized except for Hymenoptera (Figure 3.3.4). Compared to the dry season months, combined CS increased dramatically for Coleoptera (0.084 ind./trap-hours) and Hymenoptera (0.093 ind./trap-hours) and lowered for Lepidoptera (0.049 ind./trap-hours).

Temporal bat activity and, arthropod abundance and biomass showed similar trend with peaks and lows (Table 3.3.4, Table A.1, Table 2.3.1 and Figure 3.3.5). A Spearmans rank’s test revealed a weak yet significant correlation between bat activity and arthropod abundance ($r = 0.31$, $P < 001$) for the combined the data. At vegetation clutter type level, only the open vegetation yielded significant correlation between bat activity and arthropod abundance ($r = 0.41$, $P < 0.01$) whilst weaker and non-significant correlations were reported for the edge ($r = 0.01$, $P = 0.93$) and closed ($r = 0.19$, $P = 0.17$) vegetation clutter types.

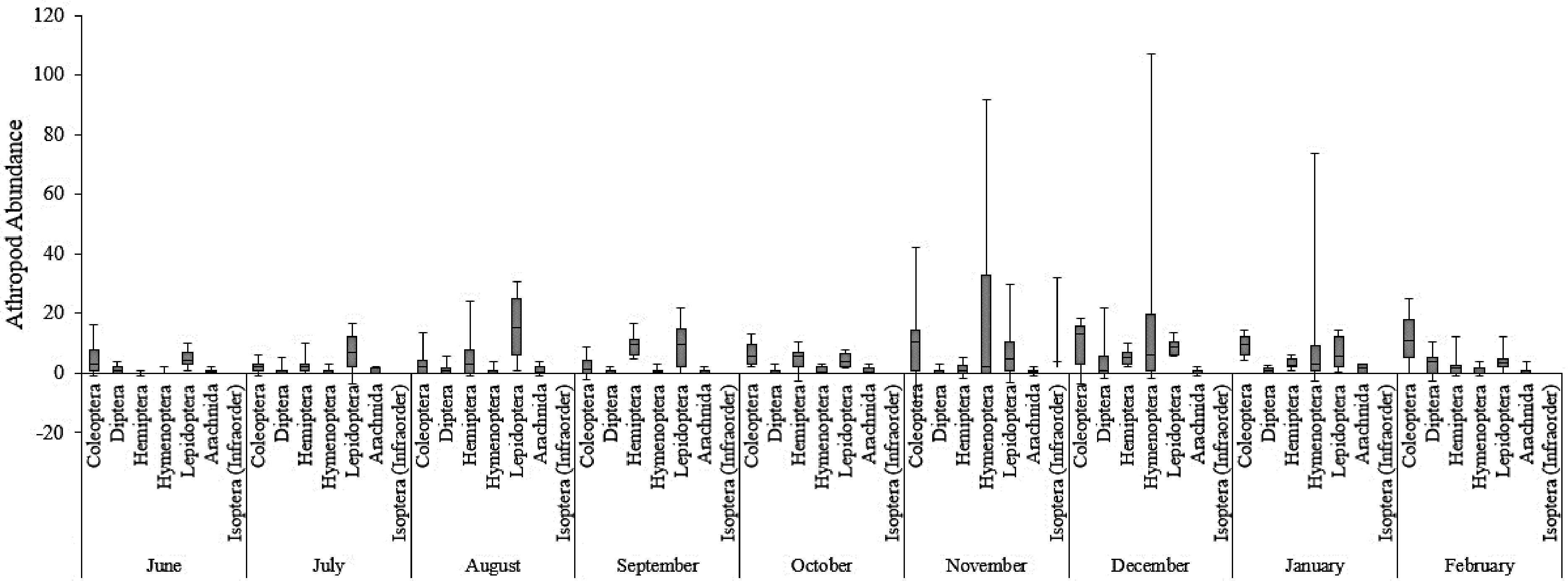

Figure 3.3.4: Box plot for the six most represented arthropod orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, Arachnida and Lepidoptera) and the Infraorder Isoptera in Meletse (data obtained from Chapter 2).

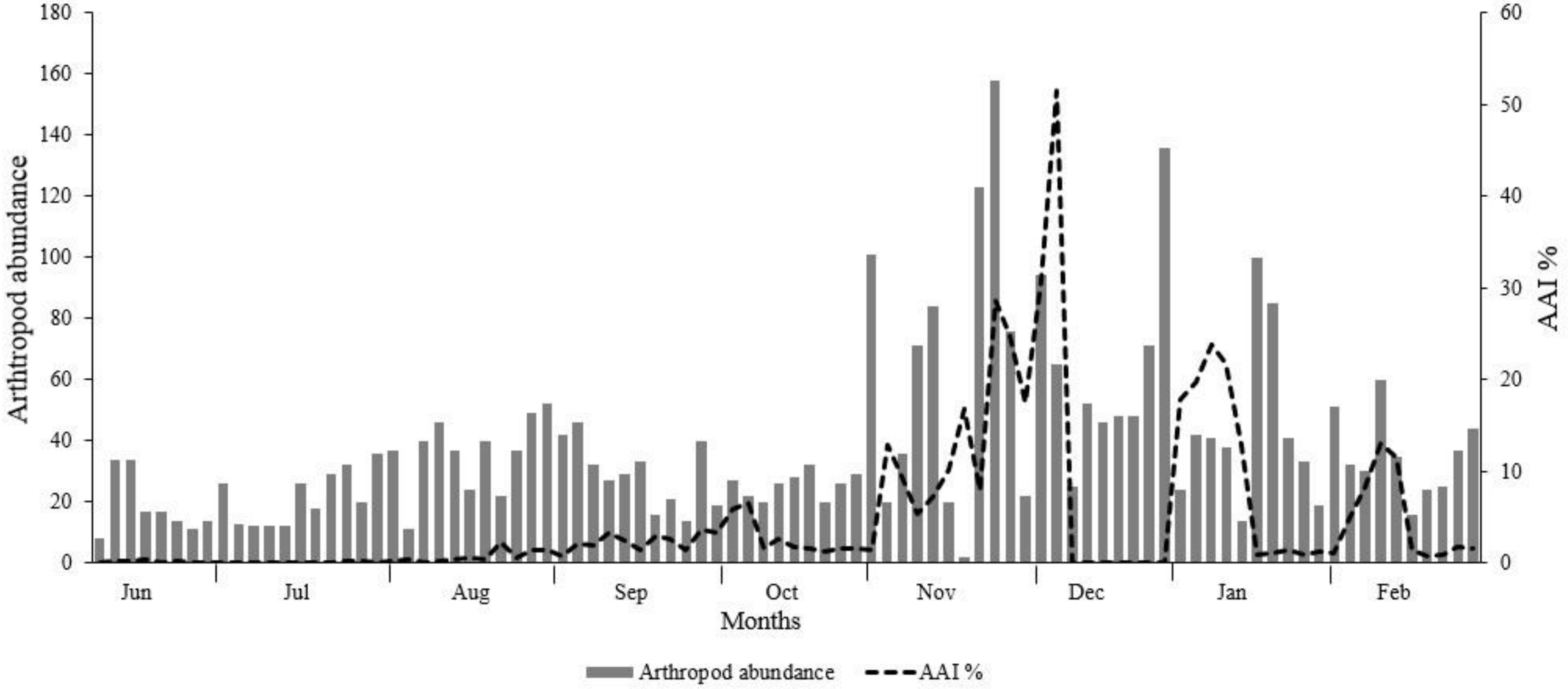

Figure 3.3.5: Monthly (June 2017–February 2018) combined arthropod abundance and bat activity collected from Meletse, Limpopo Province, South Africa.

Temporal bat activity and food resource availability for CoH WHS

Bat activity was recorded for three non-consecutive months spanning September and November 2017, and January 2018 (late dry season to wet season) at CoH WHS study area. Acoustic monitoring success was 87% after considering all nights of data loss whilst, for each month, total durations of acoustic monitoring were 405, 228 and 345 hours for September, November and January, respectively (Table 3.3.2). The AAI value for the anti-noise filter showed that bat relative activity was lowest in September (combined AAI = 9.25%, Table 3.3.5) and peaked in November (combined AAI = 15.79%, Table 3.3.5). Relative bat activity across the sampled months was not significantly different (Kruskal-Wallis ANOVA: $\chi2 = 5.45$, d.f = 2, P = 0.07). In September (late dry season), *Min. natalensis* had the highest activity (combined AAI = 1.46%, Table 3.3.5) followed by the 20–27 kHz (combined AAI = 1.05%, Table 3.3.5) and 35-45 kHz (combined AAI = 0.73%, Table 3.3.5) phonic groups.

All other species/phonic groups (14–20 kHz, 44 49 kHz, *R. blasii*, *R. clivosus*, *R. simulator* and *R. smithersi*) had AAI values below 0.5% (Table 3.3.5). In the wet season month of November, anti-noise combined AAI increased by nearly double when compared to September (Table 3.3.5). Furthermore, anti-noise mean nightly AAI increased from September (mean AAI = 0.0.31%, SD = 0.21, Table 3.3.5) to November (mean AAI = 0.83%, SD = 0.99, Table 3.3.5). However, as seen in Table 3.3.5, combined and mean nightly AAI decreased for all the species/phonic groups except for the 14–20 kHz phonic group. In addition, species/phonic group filters accounted for 43% of all the anti-noise recorded activity in September compared to just 13% in November (Table 3.3.3 and Table 3.3.5). In January, anti-noise combined and mean nightly AAIs decreased to 14.85% and 0.49% (Table 3.3.5), respectively. The highest AAI values were recorded for the 35-45 kHz (combined AAI = 1.10%, Table 3.3.5) and 20–27 kHz (combined AAI = 0.91%, Table 3.3.5) phonic groups. The species/phonic group filters accounted for 18% of anti-noise recorded activity in January (Table 3.3.3 and Table 3.3.5).

One thousand nine hundred and eight (1948) individual arthropods were collected which represented 13 taxonomic orders. The highest number of arthropods were collected in November (CS = 0.282 ind./trap-hours) and January (CS = 0.290 ind./trap-hours) whilst September yielded

Table 3.3.5: Combined and mean nightly AAI % (including standard deviation) of filtered species/phonic group recorded in September and November, 2017, and January, 2018 at CoH WHS.

	September		**November**		**January**	
	Combined AAI	**Mean nightly AAI±SD**	**Combined AAI**	**Mean nightly AAI±SD**	**Combined AAI**	**Mean nightly AAI±SD**
Anti-noise	**9.25**	0.31±0.21	**15.79**	0.83±0.99	**14.85**	0.49±0.50
Miniopterus natalensis	**1.46**	0.05±0.05	**0.39**	0.02±0.03	**0.27**	0.01±0.01
Rhinolophus blasii	**0.08**	0.00±0.01	**0.00**	-	**0.00**	-
Rhinolophus clivosus	**0.08**	0.00±0.01	**0.03**	0.00±0.01	**0.01**	0.00±0.00
Rhinolophus simulator	**0.18**	0.01±0.01	**0.03**	0.00±0.00	**0.06**	0.00±0.00
Rhinolophus smithersi	**0.13**	0.00±0.01	**0.02**	0.00±0.00	**0.03**	0.00±0.00
14–20 kHz	**0.00**	-	**0.01**	0.00±0.00	**0.00**	-
20–27 kHz	**1.05**	0.03±0.03	**0.79**	0.05±0.04	**0.91**	0.04±0.03
35–45 kHz	**0.73**	0.02±0.03	**0.62**	0.03±0.05	**1.10**	0.04±0.05
44–49 kHz	**0.21**	0.01±0.01	**0.12**	0.01±0.03	0.29	0.01±0.02

the lowest with CS = 0.172 ind./trap-hours. (Table A.1b). Despite a lower CS, biomass in January was more than twice than November at 2.98g as compared to 1.33g. Furthermore, a higher biomass was observed in September (1.87g) compared to November (Chapter 2, Table 2.3.1). The abundance and biomass proportion of the smaller sized arthropods (size A) in November was higher at 86% and 16%, respectively, compared to September and January (Chapter 2, Table 2.3.2). The largest size of arthropods was represented in September and January only comprising 24% and 45% of biomass proportions in those months. At order level, the Lepidoptera dominated captures throughout sampling (CS: September = 0.114 ind./trap-hours, November = 0.106 ind./trap-hours, January = 0.132 ind./trap-hours, Table A.1b) with maximum nightly captures consistently higher than other taxa (Figure 3.3.6). Lower and more fluctuating captures were observed for Coleoptera (CS: September = 0.013 ind./trap-hours, November = 0.065 ind./trap-hours, January = 0.045 ind./trap-hours) and Hemiptera (CS: September = 0.007 ind./trap-hours, November = 0.009 ind./trap-hours, January = 0.021 ind./trap-hours, Table A.1b).

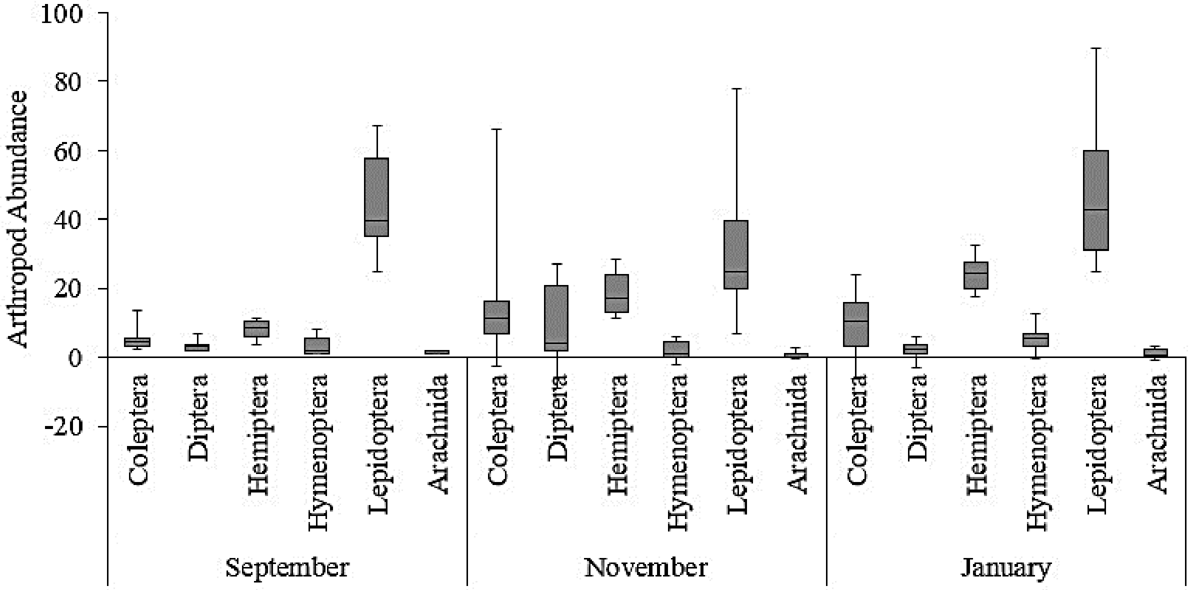

Figure 3.3.6: Box plot for the six most represented arthropod orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, Arachnida and Lepidoptera) in CoH WHS, data obtained from Chapter 2.

3.4: Discussion

Meletse temporal bat activity in relation to food availability

Temporal patterns of bat activity and arthropod abundance increased and decreased simultaneously at Meletse (Figure 3.3.5). Furthermore, the activity periods of specific species of bats were very specific to certain times of the dry and wet seasons, during which my study took place. As far as correlation is concerned, the combined data shows that temporal bat activity and arthropod availability have a weak ($r = 0.31$) yet significant ($P < 0.001$) correlation. Temporal bat activity was expectedly characterized by dry season lows and wet season peaks. In the dry season, two relatively small yet significant increases in bat activity were noted in August and September (Table 3.3.1). This coincided with a significant increase in arthropod abundance which occurred in the dry month of August (Chapter 2; Table A.1a) which stabilized in September and October. In the wet season, a large significant increase in bat activity occurred in November (Table 3.3.1) which stabilized into December and January. Similar to the dry season, another peak in arthropod abundance was recorded in November (Table A.1a).

This study at a broader scale, provides evidence of different bat species matching their temporal activity patterns with that of food resource (arthropod) availability. Bat activity peaks differed between species/phonic groups throughout the study period, coinciding with peak arthropod availability. Other studies (Churchill, 1994; Jong, 1994; Taylor & O'Neill 1988) have associated peak bat activity with maximizing profitability of critical resources including food and temperature. Jong (1994) linked different stages of the maternity season (e.g. pregnancy, nursing and weaning of young) of Eptesicus nilssoni to specific times and places where arthropod availability was high enough to meet the energy demands. Targeting periods of high food availability (arthropod abundance) to maximize food intake for maternal purposes was, for this study, evident for *Min. natalensis*, *R. simulator* and *R. blasii*. Such evidence was observed in a concurrent study by Shanahan (pers. comm, unpublished) which found females of *Min. natalensis*, *R. simulator* and *R. blasii* to be pregnant and later lactating during the wet season, using morphological examinations. Furthermore, Kearney *et al*. (2017) also found lactating females of *Min. natalensis*, *R. simulator* and *R. blasii* in an earlier study at Madimatle Cave (Gatkop Cave). Increased proportions of larger arthropods (size classes C, E, and D, Table 2.3.2) during the wet season contributed to higher biomass. The increased biomass made for higher food availability which coincided with a period of heightened energy demands by lactating female bats observed during the wet season (Jong, 1994).

With the Meletse area acting as an important maternity roosting area for the migratory Miniopteris *natalensis* (van der Merwe, 1973a, 1975). Peak activity for *Min. natalensis* coincided with peak food availability at Meletse. This species made up 57.72% of combined recorded bat data of which a majority was over November to January (Table 3.3.4), mainly due to their immigration and birthing event during this time in the Meletse area. This maximal activity coincided with the most productive period in terms of arthropod abundance and biomass (November and December - Table 2.3.1, Table 3.3.4, Table A.1). The large population of this cave dwelling migratory species utilizes the Meletse karst landscape system, specifically the Madimatle Cave (also known as Gatkop Cave–Sandspruit no. 1, van der Merwe, 1975), Rookpoort Guano Cave and Peppercorns's Cave. To give van der Merwe's (1975) account, pregnant females start the maternity season (October/November) by visiting Rookpoort Cave as a pre-maternity roost and then move to Madimatle Cave to give birth. The influx of individuals from hibernacula caves and subsequent parturition therefore explains the relatively high activity of *Min. natalensis* during the wet season (>57% of combined AAI), more especially during November to January. At the end of the maternity season (March/April), weaned young and females fly to the cooler Grassland caves of the CoH WHS karst system in Gauteng province where they hibernate for the winter (van der Merwe, 1973a; 1975).

A dramatic drop in *Min. natalensis* occurred after January (Table 3.3.4) which might imply an earlier move to the CoH WHS caves than described by van der Merwe (1975). It is not known whether the population immediately migrates to the CoH WHS caves or visits nearby caves pre-emigration. In a study of another migratory species, Ceballos *et al*. (1997) observed a predominantly male Leptonycteris curasoae population (approximately 5000) during dry season at the maternity roosting area. In the wet season, the population expanded to about 75000 as pregnant females and other males added to the population. In this study, the relatively low activity of *Min. natalensis* in the dry season and later in the wet season (February) can be attributed to individuals (mostly males) which might be residents at the Meletse caves as opposed to their migratory counterparts (Kearney *et al*., 2017; Pretorius *et al*., 2019). It is therefore likely that the maternity population of *Min. natalensis* targets a period of maximum resource availability (Churchill, 1994; Jong, 1994; Taylor & O'Neill 1988) which offered the highest abundance and biomass of arthropods (Table 2.3.1 and Table A.1a). During this period, arthropod availability primarily consisted of Coleoptera, Hymenoptera and Lepidoptera whilst lower detection of Diptera and Blattodea (Infraoder Isoptera) occurred (Table A.1a). As seen in Table 3.4.1, Findley & Black (1983) reported a *Min. natalensis* diet composition of Coleoptera (23%), Isoptera (31%) and Lepidoptera (39%). Interestingly, the only appearances of Blattodea (Infraorder Isoptera) in this study, coincided with peak *Min. natalensis* activity in November (Table 3.3.4 and Table A.1a).

The Rhinolophid species, *R. blasii*, *R. clivosus* and *R. simulator* peaked at the same time as *Min. natalensis* whilst respectively contributing only 1.12%, 0.29% and 5.09% towards combined activity. All three Rhinolophid had lower activity in the dry season which heightened in the November/December months of the wet season (Table 3.3.4). As seen in Table 3.4.1, the diet preference of Rhinolophidae species predominantly consists of Lepidoptera (Aldridge & Rautenbach, 1987; Findley & Black, 1983). Species such as *R. simulator* and *R. clivosus* were found to have a more varied diet consisting of lesser proportions of Coleoptera, Hemiptera, Hymenoptera, Isoptera, and Orthoptera (Findley & Black, 1983). The maximal availability of the preferred diet item (Lepidoptera) and, in the case of *R. clivosus* and *R. simulator*, other arthropods orders during these species' activity peaks suggests that they profited from this resource.

In September and August, *R. smithersi* and the 35–45 kHz (*Neo. capensis* and S. *dinganii*) and 44–49 kHz (*P. rusticus*/*Neo. zuluensis*) phonic groups (Table 3.3.1 and Table 3.3.4) reached their highest activity. Again, this August/September peak coincided with increase in arthropod availability. Taylor *et al*. (2012) recently split the South African distributed *R. smithersi* from *Rhinolophus hildebrandti* (Taylor *et al*., 2012). Diet information for *R. smithersi* before Taylor *et al*. (2012) therefore referred to *R. hildebrandti*. Aldridge & Rautenbach, (1987), for example, showed a predominantly Lepidoptera and, to a lesser extent, Coleoptera diet when assessing the diet of *R. hildebrandti* in Kruger National Park, South Africa. Peak activity of *R. smithersi* coincided with Lepidoptera and Coleoptera increases and the emergence of larger sized arthropods in general from this study. It is therefore strongly suspected that *R. smithersi* foraged on the highly available Lepidoptera and Coleoptera arthropods of a larger size which were available at the time.

The 35–45 kHz phonic group peaked in the latter part of the dry season and had the fourth highest activity making up 2.49% of combined detected activity. Initially, this phonic group was created to accommodate the overlapping echolocation calls of *Neo. capensis* and *Sco. dinganii* (Table 3.3.3). Monadjem *et al*. (2017) did, however, report an Fc call range of 38.0–60.8 kHz in their assessment of echolocation call parameters for *Myo. tricolor*. Taylor *et al*. (2013) found a narrower Fc call range at 45.3–62.2 kHz for *Myo. tricolor* of the Waterberg (South Africa) and Swaziland which is above the 35–45 kHz Fc range used in this study. It is therefore unclear on whether to include *Myo. tricolor* or not in the 35–45 kHz phonic group. Nevertheless, peak activity for the 35–45 kHz phonic group occurred in September (AAI = 1.30%, Table 3.3.4) and crossed into the wet season (October–December).

From a food availability perspective, the orders Coleoptera, Hemiptera and Lepidoptera had the highest CS in September (> 0.2, Table A.1a) coinciding with peak 35–45 kHz phonic group activity (Table 3.3.4). In addition, captures mostly consisted of smaller sized arthropod families (Coleoptera = smaller Scarabaeidae species; Hymenoptera = Tenthredinidae; Lepidoptera = micro Lepidoptera, smaller noctuid species, Scholtz & Holms, 1985). Aldridge & Rautenbach (1987) found mainly Coleoptera based diet in *Neo. capensis* (56%) and *Sco. dinganii* (90%) although diet composition comprised of a further 22% Lepidoptera for the former (Table 3.4.1). The more varied diet preference of *Neo. capensis*, as reported by Aldridge & Rautenbach (1987), might have prompted this species into a less specialized diet. In addition, the high availability of smaller sized arthropods possibly made up the diet of *Neo. capensis* as Aldridge & Rautenbach (1987) indicated that this species has preference for smaller prey items.

For *Sco. dinganii*, Jacobs & Barclay (2009) found a contrastingly varied diet consisting of Coleoptera (63%), Hemiptera (18%) and Lepidoptera (18%) as opposed to the more Coleoptera specialized diet reported by Aldridge & Rautenbach (1987). High captures of Coleoptera, Hymenoptera and Lepidoptera were observed during this species' peak period in the present study, therefore a wider diet variety was more likely the case as opposed to a Coleoptera specialized diet. Furthermore, the more specialized diet observed by Aldridge & Rautenbach (1987) might have been an artefact of time during which that study took place, which was at the beginning of the wet season. To explain, some species of Coleoptera, as reported by Noguera *et al*. (2017), feed on dead plant matter that is at its maximal by late dry season, which leads to high Coleoptera emergence at the end of dry season or beginning of the wet season. The observed peak activity of *Sco. dinganii* coincided with the first captures of larger sized arthropods (length >18.1mm). Considering the reported diet preference of *Sco. dinganii* (Aldridge & Rautenbach, 1987; Jacobs & Barclay, 2009), it is strongly suspected that this species targeted larger sized prey of various taxa which was evidently available at the time (Table 2.3.1, Table 3.3.4 and Table A.1a).

The 44–49 kHz phonic group likely consists of *P. rusticus* and *Neo. zuluensis*. Call characteristics for this group (Table 3.3.3) were created from *P. rusticus* (n = 3) release calls although an inspection of the calls showed an overlap with another species fitting the 44–49 kHz range. Reported Fc for *Neo. zuluensis* (Fc = 46–51 kHz, Linden *et al*., 2014; Fc = 47.2–50.81 kHz, Taylor *et al*., 2013; Fc = 40.5–46.7 kHz, Monadjem *et al*., 2017) fits the 44–49 kHz phonic group. In addition, Taylor *et al*. (2013) recorded Fc call range of 45.3–62.2 kHz (above the 35 45 kHz phonic group) for *Myo. tricolor* in the Waterberg (Lapalala). Although *Myo. tricolor* and *P. rusticus* calls are distinctly different, the former was possibly picked up by the 44–49 kHz filter owing to less strict parameters in duration (0.5–4 ms, Table 3.3.3) and slope. Nonetheless, the presence of *Myo. tricolor* at the study area has been confirmed during this study and previous records by Kearney *et al*. (2017). The diet of *P. rusticus* most likely consist of smaller sized arthropod families, with data from Aldridge & Rautenbach's (1987) pointing to Coleoptera (67%), Diptera (8%) and Lepidoptera (8%). Aldridge & Rautenbach (1987) also recorded smaller sized Coleoptera (40%) and Lepidoptera (20%) in the diet on *Neo. zuluensis*. With regards to the relatively larger *Myo. tricolor*, it is most likely that this species profited from the larger sized arthropods (Aldridge & Rautenbach, 1987).

The latter part of the wet season (January/February) presented increased proportions of the 14–20 kHz and 20–27 kHz phonic groups activity index, which coincided with arthropod availability that was nearly half of what was recorded in the November/December peak. Acoustically, Chaerephon ansorgei (Fc = 18–21 kHz, Linden *et al*., 2014; Fc = 17.8–20.5 kHz, Taylor *et al*., 2013) is suspected to be part of the 14-20 kHz phonic group. Although the are no records of *C. ansorgei* at Meletse, the closest distribution of this species was recorded by Taylor *et al*. (2013) at Lapalala in the Waterberg, Limpopo Province. To a lesser extent, *Mops midas* (Fc = 12–14 kHz, Linden *et al*., 2014; Taylor *et al*., 2013) might have also contributed to 14–20 kHz phonic group activity. As molossids, both *C. ansorgei* and *Mop. midas* are high flying (Monadjem *et al*., 2010) which emit long ranging FM calls. Despite the low hearing range (<5m) of the SD2 bat detector (Sprong *et al*., 2012), the low frequency calls belonging to these high-flying bat species were detected as they travel relatively further than high frequency calls. Despite my suspicion of these mollosids forming part of the 14–20 kHz phonic group, it is uncertain which species called within these frequencies (14–20 kHz). Nonetheless, arthropod availability was highest during the peak months of the 14–20 kHz phonic group in January and February at Meletse (Table 3.3.4). No diet information was found on *C. ansorgei*. For *Mop. midas*, Taylor *et al*. (2017) found a diverse diet consisting of, in higher counts, Lepidoptera and Coleoptera and, in lesser proportions, Blattaria (Blattodea), Diptera, Hemiptera, Neuroptera and Orthoptera.

The 20–27 kHz phonic group which made up 5.8% of combined recorded activity at the Meletse study area. South African species which call at, but not restricted to the 20-27 kHz Fc range include Chaerephon pumilus (Fc = 22–28 kHz Linden *et al*., 2014; Fc = 22.47–25.53 kHz, Monadjem *et al*., 2017), *Mops condylurus* (Fc = 25–29 kHz, Linden *et al*., 2014; Fc = 25.74–28.86 kHz, Monadjem *et al*., 2017), *Tad. aegyptiaca* (Fc = 20–24 kHz, Linden *et al*., 2014; Fc = 20.5–24.5 kHz, Taylor *et al*., 2013), *Tap. mauritianus* (Fc = 24.7–27.1 kHz; Monadjem *et al*., 2017; Fc = 24.9–27.9 kHz, Taylor *et al*., 2013; Frequency with most energy = 25kHz, Fenton & Bell, 1981). The northern part of South Africa, where Meletse is located, is part of the distribution of these four species (ACR, 2018; Monadjem *et al*., 2010). Furthermore, Chege *et al*. (2015) confirms the presence of *Tad. aegyptiaca* and *Tap. mauritianus* at the Meletse study area. The latter mentioned species (*Tap. mauritianus*) was further observed by Nkoana (pers. comm, unpublished) at a homestead during the January and February 2018 sampling events. Given the call frequency variation of bats which call within the 20–27 kHz range (Linden *et al*., 2014; Monadjem *et al*., 2017; Taylor *et al*., 2013), one cannot restrict a single species to this phonic group although, based on confirmed sightings, it is strongly suspected that these calls belonged to either *Tad. aegyptiaca* or/and *Tap. mauritianus*.

Considering the activity data for the 20-27 kHz phonic group (Table 3.3.4), it can be seen that AAI was always relatively higher at the trapping site which was utilized in August, November and February, as compared to the two other trapping sites. This is possibly due to foraging efforts being concentrated in that specific trap site for this phonic group. In terms of diet, the two possible species, *Tad. aegyptiaca* and *Tap. mauritianus*, will be considered. Schoeman & Jacobs (2003) analyzed the fecal pellets of *Tad. aegyptiaca* and revealed a diverse diet for this species (Coleoptera = 26%, Diptera = 35%, Ephemeroptera = 3%, Hemiptera = 19%, Hymenoptera = 8%, Lepidoptera = 5%, Neuroptera = 2%, Orthoptera = 0.5%, Table 3.4.1). The heightened availability of Coleoptera, Diptera, Hemiptera and Lepidoptera (Table A.1a) during both *Tad. aegyptiaca* peaks and the fact that the diet of this species has been associated with these arthropods strongly suggests that this species profited from foraging at the sampled areas at that point in time. Few studies have analyzed the diet of Tap. *mauritianus* although Monadjem *et al*. (2010) report a diet based on aerial arthropods of Coleoptera, Lepidoptera and the infraorder Isoptera.

Table 3.4.1: Diets of tested species as reported in literature cited on the right column. Coleoptera (Col), Diptera (Dip); Isoptera (Infraorder, order Blattodea); Hemiptera (Hem); Hymenoptera (Hym); Orthoptera (Ort); Neuroptera (Neu); Ephemeroptera (Eph).

	Reported diet compositions	**References**
Miniopterus natalensis	Col (20%); Iso (31%); Lep (39%)	Schoeman & Jacobs (2003)
Rhinolophus. blasii	Lep (97%)	Findley & Black (1983)
Rhinolophus clivosus	Col (29%), Lep (63%), Hem (2%), Hym (1%)	Findley & Black (1983); Schoeman & Jacobs (2003)
Rhinolophus. simulator	Col (9%); Iso (4%); Lep (77%); Ort (5%)	Findley & Black (1983)
Neoromicia capensis	Col (56%); Lep (22%)	Aldridge & Rautenbach (1987); Schoeman & Jacobs (2003)
Scotophilus dinganii	Col (90%)	Aldridge & Rautenbach (1987)
Pipistrellus rusticus	Col (67%); Lep (8%); Dip (8%)	Aldridge & Rautenbach (1987)
Tadarida aegyptiaca	Col (26%), Lep (5%), Hem (19%), Dip (35%) Hym (8%), Ort (0.5%), Neu (2%), Eph (3%)	Schoeman & Jacobs (2003)

Bat activity varies amongst the different species found at Meletse. Both bat activity and arthropod availability show that specific bat species peak at times of the year associated with peaks in arthropod availability (food resources). A likely explanation for this might be varying reproductive times for the different species found at Meletse. Shanahan (pers. comm, unpublished) caught a juvenile *Sco. dinganii* in September 2017 at Meletse. The presence of juveniles in the system points towards earlier reproductive season, likely to avoid competition with the much higher population of *Min. natalensis* during peak food availability (November–December). However, the Rhinolophid species (except *R. smithersi*) shared peak activity period with the much higher population of *Min. natalensis*. Whilst Rhinolophid species are clutter foragers whilst *Min. natalensis* are clutter–edge foragers (Norberg & Raynar, 1987; Schoeman & Jacobs, 2003, 2008– Table 3.1.1), my results show that all these species (*Min. natalensis*, *R. blasii*, *R. clivosus* and *R. simulator*) were mostly active at the edge vegetation clutter type (Table 3.3.4). Perhaps the more specialized diet of the Rhinolophids meant less competition with the more varied diet of *Min. natalensis*.

Alternatively, I propose, food availability at Meletse during the November/December peak period exceeds the foraging requirements of the bat assemblage. Microphone range limitations of the Anabat SD2 (Sprong *et al*., 2012) most likely contributed to the lower detections of all the species/phonic groups specifically ones which foraged further away from where bat detectors were deployed. The exception was *Min. natalensis* which yielded the highest AAI score due to this population's high density within the November to January period. However, low detections were expected for the other species in the area as they usually have lower density (Shanahan, pers. comm, unpublished) compared to *Min. natalensis*. In addition, the Anabat SD2 zero crossing only detects the strong portions of calls (Fenton *et al*., 2001). It is therefore likely that *Min. natalensis* calls during the peak period were detected over other species which have fainter calls. As seen in Table 3.3.4, species mentioned in the above discussion (*Neo. capensis*, *Neo. zuluensis*, *Sco. dinganii* and *P. rusticus*) with lower pitched calls as compared to *Min. natalensis* were hardly detected in the peak period. Higher pitch calls from *R. blasii* and *R. simulator* had relatively higher detections in November than those with lower pitched calls as compared to *Min. natalensis* (Table 3.3.4). This suggests that *R. blasii* and *R. simulator* were detected around the bat detector at different times to *Min. natalensis* although this requires further investigating.

Meletse bat activity across different vegetation clutter types

Bat activity and arthropod abundance varied across different levels of clutter, which supports the third hypothesis. Generally, bat activity varied across the different vegetation clutter types with activity indices either being higher or nearly the same between open, edge and closed vegetation clutter types. Temporal bat activity and arthropod availability showed a significant and weak correlation at open vegetation. The weakest correlation for these two variables was seen in the edge and closed vegetation clutter types.

Several studies have categorized bats into different feeding guilds based on their wing loading, aspect ratio and echolocation call structure (Aldridge & Rautenbach, 1987; Norberg & Rayner, 1987; Schnitzler & Kalko, 2001; Schoeman & Jacobs, 2003, 2008). Before continuing with this discussion, it is worthwhile to mention how clutter is defined in other studies. Schnitzler & Kalko

(2001) defined clutter relative to distance of vegetation/obstacles from the acoustic view of a bat, with three clutter types defined: Uncluttered, open spaces–type where bats forage far away from vegetation and catch prey on the wing (aerial feeders); Background –cluttered spaces–areas where bats forage for prey near vegetation/obstacles and either trawl or aerially hunt prey; Highly-cluttered spaces–bats hunt for prey near or on vegetation and are hence gleaners. Jantzen & Fenton (2013) defined edge as lying between forested areas and grass field. In this study, open, edge and closed vegetation clutter types were defined based on the degree of clutter within a volume of space (Figure 2.2.4). Clutter spaces were therefore defined independent of how Schnitzler & Kalko (2001) described bats acoustic perceptions when hunting for prey. Nonetheless, distinct patterns were found between open, edge and closed vegetation clutter types in both bat activity and arthropod availability.

At vegetation clutter level, there was heightened edge vegetation activity for *Min. natalensis*, *R. blasii*, *R. simulator*, R *smithersi* Ner. *capensis* (phonic group 35–45 kHz), and *Sco. dinganii* (phonic group 35–45 kHz). Activity varied less across different vegetation clutter types for the phonic groups 44–49 kHz (*P. rusticus*/*Neo. zuluensis*), 14–20 kHz and 20–27 kHz. This heightened edge activity is consistent with the findings of Jantzen & Fenton (2013) which showed higher edge activity relative to open and closed clutter areas. In addition, Jantzen & Fenton (2013) sampled along a transect line, perpendicular to a forest edge, spanning from an open field to the forest thicket. This trap placement was similar to the one employed in this study despite different trapping effort. Edge activity was most pronounced for *Min. natalensis*. In terms of foraging clutter preference, Monadjem *et al*. (2010) described *Min. natalensis* as a clutter–edge feeder based on intermediate wing loading and aspect ratio (Table 3.1.1) reported by Norberg & Rayner (1987) and Schoeman & Jacobs (2008). The high edge activity of *Min. natalensis* recorded in this study fitted with this clutter-edge description. Relatively high activity of *Min. natalensis* in November at open (AAI = 10.96%, Table 3.3.4) and closed (AAI = 8.38%, Table 3.3.4) vegetation clutter types suggests that this species utilizes various levels of clutter, possibly for foraging purposes as well.

For the 20–27 kHz phonic group (*Tad. aegyptiaca* and *Tap. Mauritianus*), the high wing loading and intermediate aspect ratio of *Tad. aegyptiaca* (Table 3.1.1) described by Schoeman & Jacobs (2003, 2008) subscribes this species to an open air foraging guild. Likewise, *Tap. Mauritianus* subscribes to an open air style of foraging due to high wing loading and intermediate aspect ratio (Norberg & Rayner, 1987; Schoeman & Jacobs, 2008) (Table 3.1.1). This open-air feeder (*Tap. mauritianus*) detects aerial prey using narrowband FM calls capable of detecting prey over a long range (Fenton *et al*., 1980; Monadjem & Reside, 2008). The highest activity for the 20-27 kHz was observed at edge and open vegetation clutter types in November and February (Table 3.3.4). The Rhinolophid species *R. simulator* had maximum activity across the different vegetation clutter types at different times of the year although it was highest at edge vegetation during the peak period (Table 3.3.4). Members of the Rhinolophidae family generally subscribe to a clutter foraging style (Norberg & Rayner, 1987). This is due to possessing low to intermediate wing loading and low aspect ratio (Table 3.1.1) as well as the ability to hover and perform slow, maneuvering flights (Norberg & Rayner, 1987). As a Rhinolophid, *R. simulator* conforms to this generalization with a low loading of 5.4 N/m2 and aspect ratio of score of 6.7 (Table 3.1.1). Monadjem & Reside (2008) also associated *R. simulator* with foraging in spaces with high cover percentage due to having a CF echolocation call.

The 35–45 kHz phonic group had the highest activity recorded in the open vegetation (Table 3.3.4). For *Neo. capensis*, Norberg & Rayner (1987) associated the relatively long wingspan, low wing loading and average aspect ratio of *Neo. capensis* with flight in open spaces. Monadjem & Reside (2008), however, linked *Neo. capensis* to clutter foraging based on this species' FM broad bandwidth echolocation call structure. The much larger Vespertiolionid, *Sco. dinganii*, has rounded wing tips, a relatively long wing span, high wing loading and aspect ratio which is associated with flight in open spaces and near clutter (Aldridge & Rautenbach, 1987; Norberg & Rayner, 1987). Calls emitted by *Sco. dinganii* have a narrow bandwidth FM part that travels longer distances (open air feeding) as well as a quasi CF part which can detect prey in low–clutter areas (Aldridge & Rautenbach 1987; Monadjem & Reside, 2008). Within the wet season months, arthropod captures (Table A.1a) were greater in open vegetation (dominated by Coleoptera, Hymenoptera and Lepidoptera) than edge vegetation (Hymenoptera only order with notable increase). It should be noted that Coleoptera captures in the closed and open vegetation arthropod captures were similar during the 35-45 kHz phonic group's activity peak. Taking into consideration the instances (October and November, Table 3.3.4) when 35-45 kHz phonic group activity was relatively high in closed vegetation and similar captures were observed for Coleoptera between open and closed vegetation (Table A.1a) throughout the peak period, perhaps these species seeks more profitable foraging spaces (Downs & Racey, 2006) which, evidently, shows tolerance for much broader types of clutter. Alternatively, the broad bandwidth FM call structure of the much smaller *Neo. capensis* (Monadjem & Reside, 2008) might exclusively place this species in the closed vegetation.

Peak activity for *R. blasii*, was more pronounced at the edge and closed vegetation. Schoeman & Jacobs (2008) described *R. blasii* as a clutter forager due to an intermediate wing loading and low aspect ratio. In addition, Monadjem & Reside (2008) associated *R. blasii* with foraging in cluttered spaces due to having a CF echolocation structure. Results from this study, however, suggest a less biased activity pattern in terms of vegetation clutter. This was not only apparent for *R. blasii* but all the other bat species and phonic groups as well. Downs & Racey (2006) showed that the species *P. pipistrellus* preferred to commute along tree edges but would cross clutter spaces to reach more profitable feeding spots (as far as 200m). Using this logic, perhaps *R. blasii* (as well as other species/phonic groups) crossed to the closed and open vegetation to feed whilst commuting at the edge. During this commuting, foraging is suspected to also take place at the edge as Downs & Racey (2006) do not imply otherwise. In the case of *R. blasii*, and generally other Rhinolophids, wing morphology (Schoeman and Jacobs, 2008) and echolocation call (Monadjem & Reside, 2008) characteristics would support a crossing to the closed vegetation clutter type.

For *P. rusticus*, the highest activity peak was observed in the open vegetation although monthly activity peaks alternated across the different vegetation clutter types. This tolerance for various vegetation clutter is explained by Norberg & Rayner’s (1987) description of *P. rusticus* (average aspect ratio and wing loading, with short, rounded wings) which allows for hawking in semi–open spaces and slow maneuvering in clutter. In another species, Jantzen & Fenton (2013) reported Lasiurus cinereus activity was predominantly less than 20m from the edge albeit this species being described as an open –air feeder (based on wing morphology). The much larger Vespertilionid, *Myo. tricolor*, with long, broad wings has intermediate wing loading (7.5 N/m2) and low aspect ratio (5.6) (Table 3.1.1). Based on these wing characteristics, Norberg & Rayner (1987) predicted a slow, agile flying around, but rarely within, clutter.

CoH WHS bat activity in relation to arthropod availability

The highs and lows in bat activity coincided with those of arthropod availability at both CoH WHS and Meletse despite fewer sampled months at the former (Chapter 2, Table A.1b, Figure 3.3.1, Figure 3.3.4, Figure 3.3.5 and Figure 3.3.6). My results therefore agree with the hypothesis which stated that bat activity will peak in response to the peak in arthropod availability at both the Grassland (CoH WHS) and Savanna (Meletse) study areas. Studies show a strong association between bat activity and arthropod availability (Churchill, 1994; Jong, 1994; Taylor & O'Neill 1988; Wang *et al*., 2010).

Activity patterns for *R. simulator*, *R. smithersi* and the 20–27 kHz, 35–45 kHz and 44–49 kHz phonic groups coincided with arthropod biomass which decreased in November and peaked in January (Chapter 2, Table 2.3.1). Arthropod biomass temporal patterns at Meletse also coincided with the activity of specific species. Although the present study does not provide such evidence, it is likely that increases in the activity of specific bat species is associated with arthropod biomass. Jones *et al*. (2009) and Wolbert *et al*. (2014) implicate temperature as a direct stimulant of bat activity. Findings by Wolbert *et al*. (2014) showed a negative relationship between bat activity and arthropod biomass and implicated temperature as being a more likely factor to influence bat activity. However, Wolbert *et al*. (2014) disregarded species level activity and rather focused on overall bat activity.

Schoeman & Jacobs (2003) reported a mixed diet consisting of similar proportions of Coleoptera, Isoptera and Lepidoptera for *Min. natalensis* (Table 3.4.1). Both study areas had a presence of these taxa during the November, except for Isoptera at CoH WHS, which makes it seem wasteful to migrate all the way to Meletse for maternity purposes. However, as Jong (1994) reported, the maternity period has greater energy demands and therefore requires greater food resources. The highest activity at the maternity roosting site of *Min. natalensis* (van der Merwe, 1973a, 1975) in Meletse also coincides with peak arthropod availability in November (Table 3.3.4). It is therefore worth comparing arthropod captures between CoH WHS and Meletse for November. Arthropod captures from Meletse were lower in abundance although nearly four times higher in terms of biomass owing to higher captures of larger sized arthropods, compared to CoH WHS (Chapter 2, Table 2.3.1 and Table A.1). Jenkins (2015) reported on the strong relationship between arthropod biomass and production. From Jenkins' (2015) viewpoint, it is therefore likely that Meletse is more productive than CoH WHS in terms of food resource availability. I therefore propose that Meletse can sustain the *Min. natalensis* population better than CoH WHS due to having higher food resource availability during the energy demanding maternity period. In addition, CoH WHS arthropod captures were higher for the softer and lighter Diptera and Lepidoptera whilst the harder and heavier Hemiptera (CS =0.047 ind./trap-hours) and Coleoptera (CS = 0.065 ind./trap-hours) had relatively lower captures (Chapter 2, Table A.1, Figure 3.3.4 and Figure 3.3.6) compared to Meletse. Higher captures of larger sized arthropods as well as harder and generally heavier taxa such as Coleoptera (CS = 0.084 ind./trap-hours) and Hymenoptera (CS = 0.093 ind./trap-hours) also attributed to the higher biomass observed at Meletse during November.

The rhinolophid species *R. blasii*, *R. clivosus*, *R. simulator* and *R. smithersi* all showed low (AAI<0.5%, Table 3.3.5) and decreasing activity (Table 3.3.5) throughout sampling at CoH WHS. Schoeman & Jacobs (2003) and Findley & Black (1983) reported a primarily Lepidoptera diet for *R. blasii*, *R. clivosus* and *R. simulator*. From a diet perspective, I therefore expected higher activity and possibly abundance of these Rhinolophids at CoH WHS compared to Meletse due to higher CS of Lepidoptera at CoH WHS (Chapter 2, Table A.1b, and Figure 3.3.6). Live trapping by Shanahan (pers. comm, unpublished) at CoH WHS study area also found low numbers of these bat species. One possibility is that these Rhinolophids roost in areas a bit further away from where I sampled which would explain the lower activity although the proximity of roosting sites is not known. The Verspertilionids in the phonic groups 35–45 kHz (*Neo. capensis* and *Sco. dinganii*) and 44–49 kHz (*P. rusticus* and *Neo. zuluensis*) showed changes throughout September to January with AAI scores below 0.5% for the latter phonic group (Table 3.3.5). Arthropod captures from CoH WHS (Chapter 2, Table A.1b, and Figure 3.3.6) supported the reported diets of mainly Coleoptera and lesser proportions of Diptera and Lepidoptera for *Neo. zuluensis*, *Neo.* Capensis and *P. rusticus* (Aldridge & Rautenbach, 1987; Schoeman & Jacobs, 2003).

3.5: Conclusion

Results from this study help to better understand how different species time their activity patterns to fit with periods of increased availability of critical resources. Such timing can be crucial for coping with energy demanding periods in the phenology of bats such as the breeding season. This information aligns with the match/mismatch hypothesis (MMH) (Durant *et al*., 2007) which states that predators maximize recruitment of offspring by matching the most energy expensive part of their breeding to peak availability of prey species. Although this study does not provide direct evidence to the MMH as bat young are nursed by females at infancy. However, Durant *et al*. (2007) did highlight the need to study weaning young as they start to directly depend on the environment for food at that stage. A recent study of the *Min. natalensis* population at Meletse by Pretorius *et al*. (2019) suggested that the need for additional energy compensation in lactating females drives the differences in mass as compared to non–lactating females and males. Taking this into consideration, perhaps the activity patterns of *Min. natalensis* and other the bat species at Meletse subscribe to the MMH.

In terms of resource availability, arthropod abundance and biomass was higher at the CoH WHS than at Meletse except for November, the peak month, when biomass at Meletse was four times the value obtained at CoH WHS. Given that the migratory species *Min. natalensis* peaked during that very month, perhaps the higher biomass better explains why this population moves from CoH WHS to Meletse. If that is the case, then an interesting question would be why this species does not remain at Meletse for the whole year. Migration in temperate bats is often associated with temperature as bats seek hibernacula roosts that offer low, stable temperatures whilst summer roosts have higher temperatures required to remain active (Moussy *et al*., 2013). Little is known about the migration of tropical bats although it is thought it is associated with fluctuating food resource availability (Fleming & Eby, 2003). The hibernacula and maternity roosting of *Min. natalensis* between CoH WHS and Meletse (van der Merwe, 1973a; 1975) is likely associated with temperature although the implications of food resource variations, as revealed in the present study, may also influence this migration. This study therefore adds knowledge to the studies on patterns of bat activity in relation to critical resources which they require to survive.

In addition, as seen in Table 3.3.4, there is evidence of tolerance for broader levels of vegetation clutter. Although it cannot be said with certainty that all the recorded activity was due to foraging activity, it is evident that species such as *Min. natalensis, R. simulator* have are active in other levels of vegetation clutter than stated by Norberg & Raynar (1987) and Schoeman and Jacobs (2008). Similar to conclusions made by Jantzen & Fenton (2013), results of this study can help in the design of future similar studies in terms of placement of bat detectors.

As mentioned previously (see 3.2 Methods, Study Areas), both study areas are on the edge of urban development. South African legislation requires the undertaking of environmental impact assessments (EIAs) to determine, assess and evaluate both negative and positive impacts of development taking into consideration natural resource base (flora and fauna) and societal needs (South Africa, 2010). I therefore recommend that any future developments should consider the findings of expert biological studies on fauna and flora within the areas. Furthermore, I agree with Struebig *et al*. (2009) that developments in such areas should consider wildlife populations on a wider landscape. I make this point giving thought to the migratory species *Min. natalensis* which relies on both Meletse and CoH WHS for its survival.

The peak period in the wet season increased the variety of diet items and generalist bat species most likely profited during this time. Although reported diet preferences (Aldridge & Rautenbach, 1987; Findley & Black, 1983; Schoeman & Jacobs, 2003) were likely the case in the wet season when such arthropods were in high abundance, I suspect species switch to a more varied diet in the dry season when there is less variety of food resources. The species specific filters used in the present study did not account for all the species found at both study areas zero crossing analysis inability to accurately capture all the characteristics in the structure of a call. Instead, zero crossing analysis only displays the highest pitch in a call (Fenton *et al*., 2001). Future studies which seek to acoustically identify species can therefore utilize time–expansion bat detectors which provide more accurate information about call structure (Fenton *et al*., 2001).

3.6: References

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Chapter 4: Conclusion and recommendations

Several studies have suggested that arthropod species composition is dependent on altitude (Adams & Bernard, 1981; Botha *et al*., 2016; Eyre *et al*., 2001; Gutiérrez & Menéndez, 1995). Botha *et al*. (2016), comparing savanna and grassland sites in South Africa, suggested that differences in arthropod species composition are due to altitude rather than biome vegetation features. However, Botha's study under represented the temporal influence of climatic conditions on vegetation and thus arthropod taxa variation (Barnett & Facey, 2016; Berridge, 2012; Pinheiro *et al*., 2002; Schowalter, 2011). In the present study, the aim was to test whether there is a temporal difference in arthropod abundance and availability between two sites namely Meletse, a savanna based site, and CoH WHS, in the grassland. This was tested by comparing arthropod abundance, biomass and taxa composition. van de Merwe (1973b, 1975) reported on the maternity roosting of a large population of *Min. natalensis* at Meletse and subsequent hibernation at CoH WHS. Studies of bats have associated food resource availability (Fleming & Eby, 2003) and climatic conditions (Moussy *et al*., 2013) as drivers of migration although little is understood about the drivers of *Min. natalensis* migration between Meletse and CoH WHS. To test this, changes in arthropod diversity and abundance (food resource) from the dry to wet season in both study sites was investigated and correlated to bat activity.

Although the results obtained in this study do not show any difference in abundance of arthropods between the two study sites, the biomass and taxa variation of the sampled arthropods was higher at Meletse. The higher biomass obtained was due to more frequent captures of larger and possibly heavier taxa such as Coleoptera and Hemiptera arthropods during the wet season (Chapter 2, Table 2.3.1, Table A.1a). These results suggests that larger arthropods are more abundant in lower altitudes. Additionally, biomass provides a snapshot estimation of productivity within a system (Jenkins, 2015). This implies that Meletse is more productive during the wet season as compared to the CoH WHS.

Biomass samples were not partitioned on a nightly basis, therefore a direct correlation between bat activity and arthropod biomass could not be undertaken in this study. However, the data presented here does support high arthropod abundance and biomass as important factors in supporting the maternity *Min. natalensis* population at Meletse. During pregnancy a bat would have to maximize foraging to meet increased energy needs for pregnancy and subsequent lactation (Churchill, 1994;

Hagar *et al*., 2012; Dinaw *et al*., 2017, Wang *et al*., 2010). The implications of larger prey items are higher energy returns during a hunt which reduces the time spent foraging for food and thus associated energy costs of flying.

Bat species including *Neo. capensis*, *Neo. zuluensis*, *R. blasii* and *R. simulator* were also found to be reproductively active at Meletse during the November 2017 to January 2018 period in a study undertaken concurrently with the present study by Shanahan (pers comm, unpublished). This overlap of reproductive effort with increased food resources links to Durant's *et al*. (2007) MMH which states that predators maximize recruitment of offspring by matching the most energy expensive part of their breeding to peak availability of prey species. Pretorius *et al*. (2019) reported that lactating females of *Min. natalensis* at Meletse had higher body mass for individuals sampled in the morning as compared to the evening. A benefit of being in an area with increased food resources during maternity season is the availability of food for weaning offspring. Although Durant *et al*. (2007) proposed that mammalian species are not good candidates for the MMH as nursing offspring do not depend directly on the food resources supplied by the environment, a consideration is made for weaning juveniles which start foraging directly from the environment (Durant *et al*., 2007). Evidence of the presence of juveniles at the Meletse system in late December and January has been recorded in previous studies at Meletse (Chege *et al*., 2015; Kearney *et al*., 2017; Shanahan, per comm, unpublished; van de Merwe, 1973b, 1975) which was when arthropod availability was found to be increased in the present study. These results suggest that arthropod availability (food resource) is a driver of *Min. natalensis* migration to Meletse as well as the activity of other bat species.

Arthropods occurrence in the karst landscapes of Meletse and CoH WHS shows their importance as foraging habitats for bats and other arthropod predators. This is evident in the degree of arthropod taxa variation, abundance and availability in relation to the variation in bat species found at both sites. The most abundant arthropod orders collected at both study sites were Coleoptera, Hemiptera, Hymenoptera and Lepidoptera (Table A.1 and Table A.3). These arthropod orders comprise of agricultural pests found in South Africa (Scholtz & Holm, 1985). These same arthropods have been associated as diet prey for many bat species found in our study (Aldridge & Rautenbach, 1987; Findley & Black, 1983; Schoeman & Jacobs, 2003, 2008). This places the bat assemblages at both Meletse and CoH WHS study as potential biological suppressors of agricultural pests found within surrounding crop lands. In addition, the migratory *Min. natalensis* also forages on pest species at other sites of its route between Meletse and CoH WHS. Taylor *et al*. (2017) reported that bats matched their activity with arthropod prey known to be agricultural pests. Future studies at Meletse and CoH WHS should focus on identifying arthropod crop pests and their associated bat predators. This should also be undertaken at other regions where the different bat species disperse or migrate in order to know the geographical area used for foraging and potentially suppressing crop pests. This will further our understanding of the economic and ecological role of these bat assemblages.

The economic and ecological contribution is periled by the impacts of land–use change. The karst landscapes in our study areas and several other natural landscapes within Gauteng and Limpopo Provinces are surrounded by land–use change impacts in the form of residential/industrial construction, crop and wildlife farming, and other development (Gibson, 2006; Grobler *et al*., 2006) which have long lasting impacts on affected areas. The impacts of land–use change have been reported in South African Grassland and Savanna biomes (Cilliers *et al*., 2004; Gibson, 2006). The mineral rich geology of Meletse has been prospected for mining (Almond, 2012). Kearney and Seamark, 2012 suggested that further development of roads, pits and processing areas resulting from the mining activities would cause the loss of foraging and drinking habitats for bat species in Meletse.

Foraging bats respond to land–use change through trophic cascading (Jones *et al*., 2009) as arthropod abundance and variation is influenced by impacts of land–use change (Birkhofer *et al*., 2015; Schowalter *et al*., 2015). Several bats (*Min. natalensis*, *Myo. tricolor*, *Neo. capensis*, *Neo. zuluensis*, P. *rusticus* and *Sco. dinganii*) found at Meletse and CoH WHS are, to a broader extent, 'generalist' feeders (Aldridge & Rautenbach, 1987; Findley & Black, 1983; Schoeman & Jacobs, 2003) and clutter–edge species (Aldridge & Rautenbach, 1987; Norberg & Raynar, 1987; Schoeman & Jacobs, 2003, 2008). 'Generalists' are relatively tolerable to more vegetation clutter types and to minor changes in prey species variation and abundance. However, Jantzen & Fenton (2013) suggest echolocation call characteristics and wing morphology may constrain the ability to utilize other vegetation clutter types. The more specialist bats such as the clutter foraging *R. blasii*, *R. clivosus*, *R. simulator* and *R. smithersi* (Schoeman & Jacobs, 2003, 2008) which primarily feed on Lepidoptera (Findley & Black, 1983; Schoeman & Jacobs, 2003) will have lower tolerance to changes, which affect prey abundance and foraging habitats. For example, removal of woody vegetation, typical to a lot of land-use activities, may negatively impact these Rhinolophids (*R. blasii*, *R. clivosus*, *R. simulator* and *R. smithersi*) as well as other high frequency clutter foraging bats such as *Cloeotis percivali* and *Hipposideros caffer*. Conversely, as shown in a study of *Myotis myotis* by Rainho *et al*. (2010), increased ground vegetation cover resulting from densely grown fodder reduces prey accessibility for gleaning bats which can either be attributed to mechanical or sensorial difficulties to capture prey. Minimizing impacts of land–use change on natural habitats is therefore important. This is reiterated in the 2020 Aichi Biodiversity targets set by the United Nations as agreed upon by stakeholder nations (Leadley *et al*., 2014). Target five and eleven of the Aichi targets are to halve the rate of loss of natural habitats and increase protected areas, respectively, by 2020. Efforts to meet these targets take into consideration the expansion of croplands and urban areas for human well–being (Leadley *et al*., 2014).

Effort to protect and prevent the loss of these natural habitats can disrupt human access to ecosystem services in the short term (Leadley *et al*., 2014). However, the trade–off of continued long term provision of these ecosystem services that will be benefited from protecting these natural habitats should be considered. From a management perspective, it is important to consider the temporal and spatial ecology of species utilizing karst landscape systems (Struebig *et al*., 2009) when implementing decisions. Areas with livestock should alternate grazing spots regularly to allow vegetation to replenish. This will in turn minimize the suppression of arthropod abundance and richness which influences their bat predators. Grazing and browsing areas can be alternated more frequently in the dry months when there is less vegetation growth and arthropod (food resource) constraints are higher for foraging bats. Browsing, in conjunction with burning, can be used as a means of controlling bush encroachment (Jordaan, 1995) the effects of which reduce prey accessibility to ground gleaning bats (Rainho *et al*., 2010).

The expansion of urban areas brings lighting which has an effect on the distribution and activity of nocturnal arthropods and their predators. The fast flying open and edge foraging bats are tolerable to the open habitat typical of lit areas (Norberg & Rayner, 1987; Rowse *et al*., 2016) thus profiting from a cluster of arthropods at an artificial light source (Fenton & Morris, 1976). However, clutter foragers such as Rhinolophids use slow, maneuverable flight (Norberg & Rayner, 1987) which can render them vulnerable to predation at an open area of a light source (Rowse *et* *al*., 2016). In addition, the short-range calls typical of clutter foragers (Norberg & Rayner, 1987) can result in orientation difficulties when hunting in these open lit areas (Rowse *et al*., 2016). Expected construction of roads and processing areas from the proposed iron mining at Meletse will reduce ground and woody vegetation cover which, as aforementioned, may negatively impact clutter foraging bats. Development of new roads should therefore aim at minimizing impact on bushy and cluttered vegetation areas. This can be done by using older road networks already established during the prospecting phase. In addition, fire breaks along the fences can be used as roads which cut straight to the main road of the area. On a broader scale, impacts to woody vegetation should be minimized in other types of developments by always keeping construction to already disturbed areas.

I recommend long term monitoring of the activity patterns of bat assemblages at Meletse and CoH WHS. Fortunately monitoring is being undertaken by AfricanBats NPC at Meletse Bat Research and Conservation Centre at Meletse through the deployment of bat detector stations at various points around the area. The advantage of bat detector stations is that they can run for long periods of time unattended. Security concerns for such expensive equipment therefore require carefull consideration as to how these devices should be deployed. Surrounding caves should also be identified as these may potentially be roosting sites for cave–dwelling bat species. In addition to bats, the arthropods and vegetation should be monitored on a regular and long term basis. Long–term monitoring of bats (predators) and arthropods (prey) within their habitats is required to gain better understanding of the temporal dynamics between predator activity and prey abundance. Such information can be used as baseline to predict the impacts of land–use change in future. Minimizing the impacts of land–use change on landscapes such as Meletse and CoH WHS will most likely result in less impact to ecosystem processes which drive these systems.

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Supplementary Tables

A: Chapter 2 and 3 supplementary tables

Table A.1: Capture success (ind./trap-hours) at (a) Meletse for combined arthropod captures (calculated against capture effort for each month) and vegetation clutter type (calculated against capture effort per trap at open, edge and closed) and (b) CoH WHS combined arthropod captures (calculated against capture effort for each month). Both (a) and (b) tables are sorted into each taxonomic order and month. Capture success was calculated against (c) capture efforts (trap-hours) at Meletse and CoH WHS for each month and per trap (in parenthesis).

(a)

		June	July	August	September	October	November	December	January	February
Total monthly CS		**0.065**	**0.081**	**0.124**	**0.108**	**0.096**	**0.267**	**0.253**	**0.175**	**0.137**
Coleoptera	**Combined**	**0.025**	**0.014**	**0.013**	**0.017**	**0.028**	**0.084**	**0.068**	**0.043**	**0.065**
	Open	0.010	0.018	0.014	0.014	0.027	0.100	0.084	0.048	0.075
	Edge	0.031	0.019	0.014	0.022	0.020	0.047	0.040	0.032	0.087
	Closed	0.034	0.005	0.013	0.014	0.037	0.106	0.081	0.048	0.032
Diptera	**Combined**	**0.005**	**0.004**	**0.005**	**0.003**	**0.003**	**0.003**	**0.024**	**0.005**	**0.024**
	Open	0.009	0.006	0.003	0.002	0.006	0.003	0.058	0.006	0.022
	Edge	0.005	0.001	0.005	0.004	0.002	0.005	0.009	0.004	0.028
	Closed	0.001	0.004	0.006	0.001	0.000	0.002	0.006	0.006	0.021
Hemiptera	**Combined**	**0.003**	**0.013**	**0.022**	**0.039**	**0.035**	**0.012**	**0.026**	**0.017**	**0.012**
	Open	0.001	0.020	0.002	0.061	0.056	0.013	0.041	0.013	0.013
	Edge	0.002	0.010	0.004	0.030	0.020	0.010	0.018	0.014	0.017
	Closed	0.006	0.009	0.060	0.025	0.029	0.014	0.019	0.023	0.007
Hymenoptera	**Combined**	**0.001**	**0.002**	**0.003**	**0.003**	**0.004**	**0.093**	**0.086**	**0.070**	**0.007**
	Open	0.000	0.001	0.001	0.001	0.006	0.167	0.129	0.047	0.010
	Edge	0.001	0.003	0.001	0.005	0.002	0.081	0.114	0.036	0.005
	Closed	0.002	0.003	0.007	0.001	0.005	0.031	0.016	0.126	0.005
Lepidoptera	**Combined**	**0.024**	**0.042**	**0.072**	**0.041**	**0.017**	**0.049**	**0.038**	**0.034**	**0.024**
	Open	0.029	0.019	0.077	0.029	0.021	0.086	0.073	0.065	0.042
	Edge	0.032	0.039	0.094	0.038	0.007	0.036	0.020	0.014	0.020
	Closed	0.010	0.070	0.045	0.057	0.024	0.024	0.020	0.024	0.009
Orthoptera	**Combined**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	**0.002**	**0.001**	**0.000**	**0.001**
	Open	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.001
	Edge	0.000	0.000	0.000	0.000	0.001	0.000	0.001	0.000	0.002
	Closed	0.000	0.000	0.003	0.000	0.000	0.006	0.001	0.000	0.000

		June	July	August	September	October	November	December	January	February
Arachnid	**Combined**	**0.002**	**0.002**	**0.007**	**0.003**	**0.003**	**0.005**	**0.005**	**0.006**	**0.003**
	Open	0.001	0.003	0.007	0.008	0.003	0.001	0.004	0.010	0.003
	Edge	0.003	0.001	0.007	0.001	0.003	0.003	0.010	0.001	0.003
	Closed	0.002	0.003	0.006	0.000	0.003	0.012	0.003	0.007	0.001
Unidentifiable	**Combined**	**0.005**	**0.001**	**0.001**	**0.003**	**0.005**	**0.002**	**0.001**	**0.000**	**0.001**
	Open	0.013	0.001	0.002	0.001	0.008	0.000	0.000	0.000	0.000
	Edge	0.000	0.003	0.000	0.003	0.003	0.001	0.003	0.000	0.001
	Closed	0.001	0.000	0.000	0.003	0.002	0.003	0.001	0.000	0.002
Mecoptera	**Combined**	**0.000**	**0.002**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	Open	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Edge	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Closed	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mantodea	**Combined**	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.001**	**0.000**	**0.000**
	Open	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000
	Edge	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000
	Closed	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Dermaptera	**Combined**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	Open	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Edge	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000
	Closed	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000
Neuroptera	**Combined**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**
	Open	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
	Edge	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Closed	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Isoptera (Infraorder of Blattodea)	**Combined**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.015**	**0.000**	**0.000**	**0.000**
	Open	0.000	0.000	0.000	0.000	0.000	0.037	0.000	0.000	0.000
	Edge	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Closed	0.000	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000
Blattodea	**Combined**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	Open	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Edge	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Closed	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000
Raphidoptera	**Combined**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.003**	**0.000**	**0.000**
	Open	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Edge	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Closed	0.000	0.000	0.000	0.000	0.000	0.000	0.008	0.000	0.000
Siphonaptera	**Combined**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	Open	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Edge	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

		June	July	August	September	October	November	December	January	February
	Closed	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ephemeroptera	**Combined**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	Open	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Edge	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Closed	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Phasmantodea	**Combined**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	Open	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Edge	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	Closed	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

(b)

	September	November	January
Total monthly CS	0.172	0.282	0.290
Coleoptera	0.013	0.065	0.045
Diptera	0.008	0.046	0.015
Hemiptera	0.022	0.047	0.065
Hymenoptera	0.007	0.009	0.021
Lepidoptera	0.114	0.106	0.132
Orthoptera	0.000	0.000	0.000
Arachnid	0.003	0.002	0.005
Unidentifiable	0.001	0.004	0.002
Mecoptera	0.003	0.001	0.000
Mantodea	0.000	0.000	0.001
Dermaptera	0.000	0.000	0.000
Blattodea	0.000	0.000	0.000
Raphidoptera	0.000	0.000	0.000

(c)

	June	July	August	September	October	November	December	January	February	Combined
Meletse	2880 (960)	2880 (960)	2880 (960)	2784 (928)	2592 (864)	2592 (864)	2400 (860)	2496 (832)	2592 (864)	24096
CoH WHS				2880 (576)		2592 (518.4)		2496 (499.2)		7968

Table A.2: Pairwise comparisons for monthly arthropod abundance between sampled months for (a) combined arthropod captures and (b) open, (c) edge and (d) closed vegetation clutter types at Meletse (Savanna). The Z-statistic and P-value (parenthesis) are reported.

(a) Combined

	June	July	August	September	October	November	December	January
July	0.456981 (0.3238)							
August	3.362399 (**0.0004**)	2.650116 (**0.004**)						
September	-2.379105 (**0.0087**)	-1.737431 (**0.0412**)	1.020412 (0.1538)					
October	-1.241764 (0.1072)	-0.724372 (0.2344)	1.928173 (**0.0269**)	-0.98953 (0.1612)				
November	-4.204422 (**0**)	-3.431674 (**0.0003**)	-0.873808 (0.1911)	1.894221 (**0.0291**)	2.73196 (**0.0031**)			
December	2.446983 (**0.0072**)	2.237908 (**0.0126**)	-1.225056 (0.1103)	1.585826 (0.0564)	1.944186 (**0.0259**)	0.916118 (0.1798)		
January	2.550733 (**0.0054**)	2.023389 (0.0215)	0.233703 (0.4076)	0.599459 (0.2744)	1.395627 (0.0814)	-0.947165 (0.1718)	1.286654 (0.0991)	
February	3.798765 (**0.0001**)	3.179718 (**0.0007**)	-0.935245 (0.1748)	1.803139 (**0.0357**)	2.555231 (**0.0053**)	0.192043 (0.4239)	0.816992 (0.207)	1.010087 (0.1562)

***P* value < 0.05**

(b) Open

	June	July	August	September	October	November	December	January
July	0.649595 (0.2579)							
August	1.705006 (0.**0440)**	1.055412 (1.0554)						
September	2.017615 (**0.0218**)	1.368020 (0.0857)	0.312608 (0.3773)					
October	0.608009 (0.2715)	-0.041586 (0.4834)	-1.096997 (0.1363)	-1.409606 (0.0793)				
November	2.523811 (**0.0058**)	1.874217 (**0.0305**)	0.818805 (0.2064)	0.506196 (0.3064)	1.915802 (**0.0277**)			
December	0.170644 (0.4323)	-0.478951 (0.3160)	-1.534362 (0.0625)	-1.846971 (**0.0324**)	-0.437365 (0.3309)	-2.353167 (**0.0093**)		
January	-1.207414 (0.1136)	-1.857009 (**0.0317**)	-2.912421 (**0.0018**)	-3.225029 (**0.0006**)	-1.815423 (**0.0347**)	-3.731225 (**0.0001**)	-1.378058 (0.0841)	
February	2.850759 (0.0022)	2.201165 (**0.0139**)	1.145753 (0.1259)	0.833144 (0.2024)	2.242750 (**0.0125**)	0.326948 (0.3719)	2.680115 (**0.0037**)	4.058174 (**0.00002**)

***P* value < 0.05**

(c) Edge

	June	July	August	September	October	November	December	January
July	0.927787							
	(0.1768)							
August	-1.241830	-2.169617						
	(0.1071)	(**0.0150**)						
September	1.725082	0.797295	2.966912					
	(**0.0423**)	(0.2126)	(**0.0015**)					
October	-0.946429	-1.874217	0.295401	-2.671511				
	(0.1720)	(**0.0305**)	(0.3838)	(**0.0038**)				
November	-1.015260	-1.943048	0.226569	-2.740343	-0.068831			
	(0.1550)	(**0.0260**)	(0.4104)	(**0.0031**)	(0.4726)			
December	-0.857522	-1.785310	0.384308	-2.582604	0.088907	0.157738		
	(0.1956)	(**0.0371**)	(0.3504)	(**0.0049**)	(0.4646)	(0.4373)		
January	-1.577382	-2.505169	-0.335552	-3.302464	-0.630953	-0.562122	-0.719860	
	(0.0574)	(**0.0061**)	(0.3686)	(**0.0005**)	(0.2640)	(0.2870)	(0.2358)	
February	-0.414421	-1.342209	0.827409	-2.139504	0.532008	0.600839	0.443101	1.162961
	(0.3393)	(0.0898)	(0.2040)	(**0.0162**)	(0.2974)	(0.2740)	(0.3288)	(0.1224)

***P* value < 0.05**

(d) Closed

	June	July	August	September	October	November	December	January
July	3.232199							
	(**0.0006**)							
August	1.517155	-1.715044						
	(0.0646)	(**0.0432**)						
September	0.969373	-2.262826	-0.547782					
	(0.1662)	(**0.0118**)	(0.2919)					
October	2.617020	-0.615179	1.099865	1.647647				
	(**0.0044**)	(0.2692)	(0.1357)	(**0.0497**)				
November	1.696403	-1.535796	0.179248	0.727030	-0.920617			
	(**0.0449**)	(0.0623)	(0.4289)	(0.2336)	(0.1786)			
December	-0.061661	-3.293860	-1.578816	-1.031034	-2.678681	-1.758064		
	(0.4754)	(**0.0005**)	(0.0572)	(0.1513)	(**0.0037**)	(**0.0394**)		
January	2.946836	-0.285363	1.429682	1.977463	0.329816	1.250434	3.008498	
	(0.0016)	(0.3877)	(0.0764)	(**0.0240**)	(0.3708)	(0.1056)	(**0.0013**)	
February	1.065450	-2.166749	-0.451705	0.096077	-1.551570	-0.630953	1.127111	-1.881386
	(0.1433)	(**0.0151**)	(0.3257)	(0.4617)	(0.0604)	(0.2640)	(0.1298)	(**0.0300**)

***P* value < 0.05**

Table A.3: Percentage proportions (%) of caught arthropod individuals from Meletse (Savanna) sorted into each taxonomic order and month (June–February) for combined captures and each vegetation clutter type (open, edge and closed).

		June	July	August	September	October	November	December	January	February	Grand Total
Coleoptera	Combined	39	17	11	15	29	32	27	24	47	27
	Open	16	26	13	12	21	25	21	25	45	24
	Edge	42	23	11	21	32	26	19	32	53	28
	Closed	60	5	9	14	37	51	52	21	42	31
Diptera	Combined	8	5	4	2	3	1	10	3	17	6
	Open	15	9	3	2	5	1	15	3	13	7
	Edge	7	1	4	4	4	3	4	4	17	6
	Closed	2	4	4	1	0	1	4	3	27	4
Hemiptera	Combined	5	16	18	36	36	5	10	10	9	14
	Open	2	29	2	53	44	3	11	7	8	14
	Edge	3	13	3	29	32	6	8	14	11	11
	Closed	11	10	43	24	29	7	12	10	9	17
Hymenoptera	Combined	2	3	3	2	4	35	34	40	5	20
	Open	0	2	1	1	5	41	33	25	6	21
	Edge	1	4	1	5	4	44	53	35	3	21
	Closed	4	3	5	1	5	15	10	54	6	16
Lepidoptera	Combined	37	52	58	38	18	18	15	20	17	27
	Open	46	28	72	25	17	21	19	34	25	27
	Edge	43	48	75	36	11	19	9	14	12	28
	Closed	18	73	32	56	24	12	13	10	12	25
Orthoptera	Combined	0	0	1	0	0	1	0	0	1	0
	Open	0	0	1	0	0	0	0	0	1	0
	Edge	0	0	0	0	2	0	1	0	1	0
	Closed	0	0	2	0	0	3	1	0	0	1
Arachnid	Combined	3	3	6	3	4	2	2	3	2	3
	Open	2	5	7	6	3	0	1	5	2	3
	Edge	4	1	6	1	6	2	5	1	2	3
	Closed	4	3	4	0	3	6	2	3	1	3
Unidentifiable	Combined	7	2	1	2	5	1	0	0	1	1
	Open	20	2	2	1	6	0	0	0	0	2
	Edge	0	4	0	3	6	1	1	0	1	1
	Closed	2	0	0	3	2	2	1	0	3	1
Mecoptera	Combined	0	2	0	0	0	0	0	0	0	0
	Open	0	0	0	0	0	0	0	0	0	0
	Edge	0	5	0	0	0	0	0	0	0	0
	Closed	0	1	0	0	0	0	0	0	0	0
	Combined	0	0	0	0	1	0	0	0	0	0

		June	July	August	September	October	November	December	January	February	Grand Total
Mantodea	Open	0	0	0	0	0	0	1	0	0	0
	Edge	0	0	0	0	4	0	0	0	0	0
	Closed	0	0	0	0	0	0	0	0	0	0
Dermaptera	Combined	0	0	0	1	0	0	0	0	0	0
	Open	0	0	0	0	0	0	0	0	0	0
	Edge	0	0	0	1	0	0	0	0	0	0
	Closed	0	0	0	1	0	0	0	0	0	0
Neuroptera	Combined	0	0	0	0	0	0	0	0	1	0
	Open	0	0	0	0	0	0	0	0	1	0
	Edge	0	0	0	0	0	0	0	0	0	0
	Closed	0	0	0	0	0	0	0	0	0	0
Isoptera	Combined	0	0	0	0	0	6	0	0	0	1
	Open	0	0	0	0	0	9	0	0	0	2
	Edge	0	0	0	0	0	0	0	0	0	0
	Closed	0	0	0	0	0	4	0	0	0	1
Blattodea	Combined	0	0	0	0	0	0	0	0	0	0
	Open	0	0	0	0	0	0	0	0	0	0
	Edge	0	0	0	0	0	0	0	0	0	0
	Closed	0	0	0	0	0	1	0	0	0	0
Raphidoptera	Combined	0	0	0	0	0	0	1	0	0	0
	Open	0	0	0	0	0	0	0	0	0	0
	Edge	0	0	0	0	0	0	0	0	0	0
	Closed	0	0	0	0	0	0	5	0	0	1
Siphonaptera	Combined	0	0	0	0	0	0	0	0	0	0
	Open	0	0	0	0	0	0	0	0	0	0
	Edge	0	0	0	0	0	1	0	0	0	0
	Closed	0	0	0	0	0	0	0	0	0	0
Ephemeroptera	Combined	0	0	0	0	0	0	0	0	0	0
	Open	0	0	0	0	0	0	0	0	0	0
	Edge	0	0	0	0	0	0	0	0	0	0
	Closed	0	0	0	0	0	0	0	0	0	0
Phasmantodea	Combined	0	0	0	0	0	0	0	0	0	0
	Open	0	0	0	0	0	0	0	0	0	0
	Edge	0	0	0	0	0	0	0	0	0	0
	Closed	0	0	0	0	0	0	0	0	0	0

Table A.4: Descriptive statistics (Mean ± standard deviation(SD), minimum–maximum) for arthropod individuals collected at (a) Meletse and (b) CoH WHS. Abundance for each sampled month sorted into combined samples (n=30), vegetation clutter type (n=10–Meletse only), including grand total (n=270–Meletse; n = 90–CoH WHS).

	Meletse									
	June	July	August	September	October	November	December	January	February	Grand Total
Combined	19±4.44	23±9.92	36±13.01	30±10.83	25±4.41	69±50.02	61±33.81	44±27.73	35±13.25	38±27.88
	8–34	12–37	11–52	14–46	19–32	2–158	22–136	14–100	16–60	2–158
Open	6±2.31	7±3.24	10±5.89	11±5.14	11±4.36	35±30.30	31±21.08	16±0.02	15±7.74	16±16.16
	1–11	1–12	2–20	5–19	5–20	1–91	8–72	2–37	6–28	1–91
Edge	7±2.42	8±5.5	12±6.16	10±6.27	5±1.77	16±19.23	17±20.62	9±4.55	14±10.74	11±11.11
	2–18	2–20	2–12	3–10	2–8	1–68	5–75	2–17	5–25	1–75
Closed	6±4.85	9±8.84	14±4.84	10±2.87	9±2.87	18±5.82	12±15.20	20±2.95	7±8.71	11±2.26
	0–14	3–19	1–32	3–16	6–16	0–31	5–24	4–47	3–11	0–47
	CoH WHS									
Combined				16.00±6.24		24.00±18.69		24±14.05		36±31.11
				5–30		8–90		6–69		6–129

Table A.5: Vegetation clutter assessment undertaken for site (a) site A, (b) site B and (c) site C. Clutter scores: 1 (very sparse, <10% cover); 2 (sparse, 10-29%); 3 (moderate, 30-49%); 4 (mid-dense, 50-69%); 5 (dense, >70%).

(a)

	Vegetation clutter type											
	open				edge				closed			
Plot number	1	2	3	4	1	2	3	4	1	2	3	4
Dominant grass	*Pogonarthria squarrosa*	*Enneapogon cenchroides*	*Enneapogon pretoriensis*	*Pogonarthria squarrosa*	*Aristida canescens*	*Aristida congesta*	*Aristida congesta*	*Aristida congesta*	*Enneapogon cenchroides*			*Aristida congesta*
Dominant shrub												
Tree												
Ground layer (0 - 0.5m)	65	75	60	75	60	30	70	80	60	60	30	80
Clutter score	4	5	4	5	4	3	4	4	4	4	3	4
Shrub layer (0.5-1m)	30	25	30	50	35	0	50	30	60	30	10	60
Clutter score	3	2	3	4	3	1	4	3	4	4	2	4
Mid-storey (1-2m)	1	0	0	0	8	0	30	40	55	15	2	50
Clutter score	1	1	1	1	1	1	3	3	4	2	1	4
Max (>2m)	0	0	0	0	0	0	0	0	50	5	0	40
Clutter score	1	1	1	1	0	0	0	0	50	5	0	40
Ground cover %	75	90	60	80	60	40	70	70	90	65	10	90
Tree Height (m)	5	5	4	5	4	3	5	5	5	4	2	5
Canopy height	0	0	0	0	0	1.5	0	3	1.5	0	0	1.5
Canopy width	0	0	0	0	0	2	0	2	4	0	0	4

(b)

	Vegetation clutter type											
	open				edge				closed			
Plot number	1	2	3	4	1	2	3	4	1	2	3	4
Dominant grass	*Eragrostis trichophora*	*Eragrostis trichophora*	*Eragrostis trichophora*	*Chloris virgata*	*Themeda triandria*	*Themeda triandria*	*Themeda triandria*		*Hetepogon contortus*	*Hetepogon contortus*	*Schizachyrium jeffreysii*	*Hetepogon contortus*
Dominant shrub												
Tree											*Dichrostachys cinerea*	
Ground layer (0 - 0.5m)	40	20	40	15	100	60	20	70	90	60	60	
Clutter score												
Shrub layer (0.5-1m)	0	0	0	0	75	50	60	0	40	10	10	80
Clutter score												
Mid-storey (1-2m)	0	0	0	0	60	10	40	0	0	10	65	60
Clutter score												
Max (>2m)	0	0	0	0	45	0	20	0	0	40	70	40
Clutter score	1	1	1	1	3	1	2	1	1	3	5	3
Ground cover %	40	30	30	30	90	40	100	0	70	100	100	100
Tree Height (m)	0	0	0	0	3	1.5	3.5	0	0	2	2	1
Canopy height	0	0	0	0	1.5	1.5	2.5		0	0	0	1
Canopy width	0	0	0	0	2.5	1.5	3.5		0	0	0	1

(c)

	Vegetation clutter type											
	open				edge				closed			
Plot number	1	2	3	4	1	2	3	4	1	2	3	4
Dominant grass					*Pogonarthria squarrosa*	*Arastida canensis*	Pogonarthria squarrosa		*Aristida canescens*	*Aristida canescens*	*Tricholaena monachne*	*Tricholaena monachne*
Dominant shrub					-	*Dichrostachys cinerea*	*Dichrostachys cinerea*		-	*Euclea crispa*	-	*Euclea crispa*
Tree	60	20	50	65								
Ground layer (0 - 0.5m)					60	80	85		70	80	70	90
Clutter score	0	0	0	0								
Shrub layer (0.5-1m)					20	10	10		50	70	70	80
Clutter score	0	0	0	0								
Mid-storey (1-2m)	90	70	80	90	15	0	0		40	20	50	30
Clutter score												
Max (>2m)	60	20	50	65	5	0	0		0	0	10	30
Clutter score	1	1	1	1	1	1	1		1	1	2	3
Ground cover %	80	75	90	90	70	70	80	90	60	90	80	90
Tree Height (m)	0	0	0	0	0	0	0	0	0	0	2.5	0
Canopy height	0	0	0	0	0	0	0	0	0	0	2.5	0
Canopy width	0	0	0	0	0	0	0	0	0	0	2	0