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Molete, Letsema Mahlatse Tilly

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DIETARY FLEXIBILITY OF FREE-LIVING BAT-EARED FOXES IN A SEMI-ARID ENVIRONMENT

Letsema Mahlatse Tilly Molete

A Dissertation submitted to the Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Master of Science.

Johannesburg, South Africa, September 2021

DECLARATION

I, Letsema Mahlatse Tilly Molete declare that this thesis is my own, unaided work. It is being submitted for the Degree of MSc Physiology in the Faculty of Health Science at the University of the Witwatersrand, Johannesburg. The work herein has not been submitted before for any degree or examination at any other University.



(Letsema Mahlatse Tilly Molete)
Signed on the 8th day of September 2021

I certify that all procedures used in this dissertation were approved by the University of the Witwatersrand Animal Research Ethics Committee (AREC; 2019/04/21 CL) and the Department of Environment and Nature Conservation, Northern Cape (permit OBD 1346/2019).

ABSTRACT

Climate change is influencing environmental temperatures and rainfall, affecting species' functioning and survival across the globe, through direct and indirect impacts. In much of southern Africa, increasing air temperatures and greater variability in rainfall are occurring, with droughts likely to become more common. An indirect consequence of these climatic changes is a change in the availability of food resources for animals. In recent years in the arid zone Kalahari, a decline in ant and termite numbers (as reflected by pitfall traps) has been associated with starvation and reduced reproductive output in aardvarks (*Orycteropus afer*) and pangolins (*Smutsia temminckii*), both specialist feeders on ants and termites (myrmecophagous mammals). Bat-eared foxes (*Otocyon megalotis*) are also myrmecophagous mammals found in the Kalahari and other semi-arid and arid regions of eastern and southern Africa. Bat-eared foxes alter the structure of vegetation when digging for prey and control the termite populations in an area by consuming large numbers of these insects. Bat-eared foxes also are known to influence the dynamics of disease in an ecosystem by being a vector to several viruses. Comparable to aardvarks, their preferred prey is the Northern harvester termite (*Hodotermes mossambicus*). However, unlike aardvarks and pangolins, bat-eared foxes have been shown to have a much more generalist diet, and feed on other invertebrates as well as plants, and even reptiles and small mammals. It is established that animals with a generalist diet are likely to be better off in changing environments than are specialist feeders. To determine whether bat-eared foxes are likely to cope better with the effects of climate change in the Kalahari compared to aardvarks and pangolins, I investigated the seasonal dietary flexibility of bat-eared foxes at a time when long-term pitfall trap monitoring at my study site (Tswalu Kalahari Reserve) had revealed low availability of their preferred prey (*H. mossambicus*). I assessed the diet of bat-eared foxes over that year using collected scats from bat-eared foxes from March 2019 to March 2020 and described the availability of invertebrates using pitfall traps. I further investigated whether there was a seasonal change in the active periods of bat-eared foxes by observations of their activity periods over the year. During the year of study, Tswalu experienced lower than average rainfall, impacting the grass productivity and invertebrate prey availability. There was no linear relationship between rainfall and grass cover, or between environmental temperatures and grass cover. The numbers of invertebrates in pitfall traps did not correlate with grass cover or rainfall. Ants were by far the most common item found in the traps, occurring at about 35-fold

the numbers of termites. Despite the apparent low number of termites, as reflected by the traps, bat-eared foxes consumed harvester termites throughout the year, with termites comprising more than half of their diet in all seasons. Ants made up almost a quarter of the dietary items, while bat-eared foxes also consumed other invertebrates as well as plants. Bat-eared foxes changed their activity period seasonally, being more diurnal in the cooler months, possibly to overlap with the activity of their preferred prey. Despite the low numbers of termites found in traps, bat-eared foxes were able to locate and continue to feed preferentially on harvester termites. Their ability to source termites and their dietary flexibility indicate that the bat-eared fox may be able to cope relatively well with the ongoing and predicted effects of climate change in the Kalahari.

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CHAPTER 1

INTRODUCTION

Global climate change is influencing environmental temperatures, rainfall, and weather patterns, with impacts on species diversity and potential species extinction (Thomas et al., 2004; Urban, 2019). Much of southern Africa is expected to become hotter and drier, with the warming of temperatures expected to be greater than 4°C in many regions in the 21st century (Collier et al., 2008; Engelbrecht et al. 2015). Maximum daily temperatures already have increased substantially in arid zones of southern Africa, including in the Kalahari by 1.7°C (van de Ven et al., 2020). Recent research has shown that with ongoing climate change, hot and dry conditions in the Kalahari led to aardvarks (*Orycteropus afer*) starving, with potential implications for their survival in the region (Rey et al., 2016; Weyer et al., 2020). Aardvarks in the Kalahari specialized their diet on harvester termites (*Hodotermes mossambicus*) and did not shift to alternative food sources when these termites became unavailable to them during periods of drought (Weyer et al., 2020). Another mammal in the Kalahari that consumes the same harvester termites in its diet (Nel, 1978; Koop and Velimirov, 1982; Jumbam et al., 2019) is the bat-eared fox *(Otocyon megalotis)*. Bat-eared foxes typically consume harvester termites when the termites are readily available to the foxes (Jumbam et al., 2019). However, they have greater dietary breadth than aardvarks, feeding on other items such as ants, beetles and their larvae, grasshoppers and fruits, seeds, spiders, frogs, and bird nestlings (Lamprecht, 1979; Berry, 1981; Koop and Velimirov, 1982; Kuntzsch and Nel, 1992; Klare et al., 2011; Grant and Samways, 2014). It has been argued that species with more generalist diets will cope better with climate change than will specialist feeders (de Vries et al., 2011; Smit and Reeves, 2012; Weyer, 2018; Levy et al., 2019). Whether bat-eared foxes in the Kalahari will cope when their most utilized prey species decreases in availability is not known.

Following a period where long-term monitoring of insect availability in the Kalahari had revealed a substantial decline in termite availability (data compiled by the Kalahari Ecosystem Endangered Project). I initiated my study to investigate whether bat-eared foxes, which are considered obligate termite feeders, would be able to buffer themselves against the consequences of climate change on food availability through dietary flexibility. I examined how the diet of bat-eared foxes and availability of potential dietary species varied across one year in the Kalahari of South Africa. I consider the implications of my results for the future survival of bat-eared foxes facing climate

change, as well as the implications for other myrmecophagous mammals (species that specialize on ants and termites) in the region.

1.1 Climate change

1.1.1 Global climate change

Current global climate change is a consequence of anthropogenic influences (Karl and Trenberth, 2003; Crowley, 2000). The increase of temperatures and levels greenhouse gases, such as carbon dioxide and methane have been rising since the industrial revolution (Hulme, 2005; Collier et al., 2008; Thomas et al., 2019). Global temperatures have increased by approximately 0.85ºC and carbon dioxide has increased by ~40% since the 1850s preindustrial period (Hulme, 2005; van der Geest et al., 2019). Should current trends continue without mitigation, temperatures are predicted to continue to increase by 0.3ºC every decade (Karl and Trenberth, 2003; Melillo et al., 2011). In the northern hemisphere warmer temperatures are becoming evident, with decreasing frost occurrence (Alexandra et al., 2006; Kreuzwieser and Gessler, 2010), increasing rainfall during winter, and occurrence of floods during spring (Kreuzwieser and Gessler, 2010). In the southern hemisphere warmer temperatures are being experienced with reduced occurrence of cold days (Conway, 2006) and increased frequency of droughts and heat waves (Alexandra et al., 2006; Melillo et al., 2011; du Plessis et al., 2012).

Temperature and rainfall patterns impact the productivity, biodiversity and adaptation of species inhabiting a region (Kreuzwieser and Gessler, 2010; Urban, 2019; Thomas et al., 2004). Accordingly, many of the environmental changes that occur around the globe caused by climate change may lead to disintegrated ecosystems, possibly increasing the rate of species extinction (Adger et al., 2005; Urban, 2019). Ecosystems globally respond to climatic changes differently (Turner et al., 2020), with the capacity of ecosystems to respond depending on the ability of organisms to adapt to climate drivers (Schneider, 1992). Mammal species may adapt to thermoregulatory stressors from climate change through phenotypic plasticity and microevolution (Boyles et al., 2011). Microevolution can sustain populations of mammals through genotypic changes resulting from alleles with favourable characteristics (Phillimore et al., 2010), while phenotypic plasticity resulting from physiological, morphological or behavioural

changes may enable individuals to adapt to some of the consequences of climate change (Donnelly et al., 2012). Increasing temperatures, especially in already hot environments, are expected to affect terrestrial and aquatic ecosystems by changing the structure of the ecosystem and biodiversity of species (Shukla et al., 2019; Turner et al., 2020). Terrestrial ecosystems will likely be impacted through increased droughts, wildfires, more varied rainfall, and increased temperature (Shukla et al., 2019; Turner et al., 2020). Species that inhabit ecosystems affected with drought are likely to be vulnerable, in turn impacting trophic levels of the ecosystem (Shukla et al., 2019; Turner et al., 2020). Grassland ecosystems depend on fire and rainfall for productivity; the lack of rainfall and fire occurrence often leads to a decrease in species composition in grasslands and may transition grasslands to woody ecosystems (Boakye et al., 2013; Shukla et al., 2019). Monitoring species and ecosystems is essential for reducing the impact of climate change on biodiversity and conserving species.

1.1.2 Climate change in Africa and southern Africa

The large continental land mass of Africa has varying climatic conditions from the North to the South, with regions that are likely to be severely impacted differently by climate change (Collier et al., 2008; Thomas and Nigam, 2018). Temperatures in Africa have increased by at least 0.5 ºC per decade since the 20th century and will further increase in the future, impacting rainfall occurrence (Nkomo et al., 2008). There are three main climate drivers that influence climatic changes in Africa, namely the Intertropical Convergence Zone, the El Niño Southern Oscillation, and the West African Monsoon. These three climate drivers have impacted African regions by reducing moisture and increasing temperatures in tropical and subtropical regions (Conway, 2006). The Intertropical Convergence Zone causes fluctuation of rainfall patterns north and south of the African equator (Nkomo et al., 2006). The intertropical convergence is caused by the intersect of warm dry north-easterly winds and moist south-easterly winds (Nicholson, 2018), which influences humidity and cloud formation resulting in rainfall occurrence (Thomas and Nigam, 2018; Timmermann et al., 2018). The Intertropical Convergence Zone causes the equator and tropics to experience wet seasons with high temperatures and humidity (Obiero and Onyando, 2013), and the northern regions to experience strong heat stress occurring more than in the southern regions of Africa (Parkers et al., 2019). An absence of the Intertropical Convergence Zone increases the likelihood of droughts occurring in southern Africa while occurrence of the

Intertropical Convergence Zone in northern Africa influences the occurrence of floods (Conway, 2006). The El Niño Southern Oscillation is distinguished by the fluctuation of surface warming and equatorial winds, which affects the tropic and subtropic warming temperatures (Timmermann et al., 2018). The El Niño Southern Oscillation is a climatic and oceanographic phenomenon which has extreme effects on terrestrial ecosystems, particularly in arid and semi-arid regions (Holmgren et al., 2006). The West Africa Monsoon is caused by south-westerly wind during warmer months and north-easterly winds during cooler months in the year, which characterises the dynamics of tropic and subtropical reversal of surface winds and rainfall variation in west Africa (Conway, 2006). Understanding these African climatic drivers in the context of climate change is essential to better understand the impacts on African ecosystems, species resilience, adaption, and survival abilities (Nkomo et al., 2006), and to manage ecosystems for sustainability of species (Conway, 2006; Turner et al., 2020).

During the 21st century, regions of northern and southern Africa are expected to become hotter and drier, with an increase of temperatures by as much as 4-6 ºC, while the tropics are likely to have a temperature increase of 3-5 ºC and reduced rain occurrence of ~10% to 20% (Conway and Schipper, 2010; Warnatzsch and Reay, 2019). In east and central African regions rainfall is expected to increase by at least 15% (Collier et al., 2008; Jury, 2013; Engelbrecht et al., 2015). Climate change will intensify the impact on surface temperature and availability of water on current environmental ecosystems, which will further imperil wetlands, aquatic ecosystems, and terrestrial ecosystems and species that rely on these ecosystems (Warnatzsch and Reay, 2019). Regions of Sub-Saharan Africa are most vulnerable to the impacts of climate change, with Malawi, Sahel and the Horn of Africa thought to be the most vulnerable to drought and an increase in temperatures (Conway and Schipper, 2010; Warnatzsch and Reay, 2019; Parkers et al., 2019). The increase of temperatures and rainfall distribution trends under climate change will affect Northern and Central Africa with heat stress events, particularly in the Sahel (Parkers et al., 2019).

In southern African semi-arid environments, climate change has caused the regions to become hotter and drier with increasing frequency of drought (Jury, 2012; Holmgren et al., 2006; Engelbrecht et al., 2015), and the impacts have been observed in various ecological systems (Adger et al, 2005). Drier and hotter environmental conditions in arid and semi-arid southern Africa are partly the result of the Pacific El Niño Southern

Oscillation phenomenon (Collier et al., 2008). Species inhabiting arid areas are impacted by the increase in temperatures influenced by climate change (Smit et al., 2016). Increased carbon dioxide from climatic changes has impacted the productivity of plants, with impacts for the nutritional needs of animals (Melillo et al., 2011). The intensity of atmospheric carbon dioxide will change plant water usage and the efficiency of photosynthesis in plants, as well as stomatal opening, further altering ecosystems, ecosystems metabolisms and impact trophic levels within ecosystems (Smit et al., 2016).

Southern African savanna ecosystems of the Kalahari, specifically, are experiencing hotter and drier weather through climate change (Holmgren et al., 2006; Rey et al., 2017). In 2013, environmental temperatures in the Kalahari had increased by 3˚C since the 1980s, compared to the preceding 35 years mean environmental temperature (Rey et al., 2017). The increase in environmental temperatures in the Kalahari has been associated with more frequent occurrences of drought (Rey et al., 2017; Weyer, 2018). The consequences of hotter and drier weather in semi-arid regions are typically seen in the phenology of animals, with animals responding by changing the timing of events such as reproduction (Tews et al., 2004; Vetter, 2009). Climate change also can challenge the ability of mammals to maintain homeostasis (Fuller et al., 2016), requiring animals to alter their physiology and behaviour to cope with the change (Holmgren et al., 2006). The body size of mammals influences their physiological tolerance of heat load; small mammals can tolerate heat exposure for shorter periods compared to larger mammals (Fuller et al., 2012). Small mammals have a relatively larger surface area to volume ratio, so gain heat and dehydrate more rapidly in a hot environment compared to larger mammals (Pearson, 1975; Lima et al., 2002; Fuller et al., 2021). Should increases of environmental temperatures continue, body temperature in active small mammals may increase further, with impacts on their survival (Fuller et al., 2021). When ecosystems and habitats have a supply of water, larger dryland mammals (about 15kg to ~1000kg) can regulate body temperatures between 1 to 2˚C, over 24 h (Fuller et al., 2016). Large dryland mammals make use of evaporative cooling to maintain homeothermy (Fuller et al., 2021). Under climate change, the continued alteration of ecosystems is expected to impact rare and endangered species, with probable extinction occurrence (Isik, 2011; Melillo et al., 2011). Rare and endangered species are often at risk of survival under climate change as they have smaller population sizes, with lower reproduction success in some cases

and low genetic variations (Isik, 2011). Understanding climate change and the impact it has on animals and their habitats is therefore important for the conservation of species biodiversity and management of ecosystems (Varner and Dearing, 2014).

1.2 Potential effects of hotter and drier conditions resulting from climate change on African mammals in drylands

Arid and semi-arid dryland regions cover ~30% to 40% land around the globe (Lioubimtseva, 2004; Singh and Chudasama, 2020; Fuller et al., 2021). They typically experience high temperatures and low mean rainfall, with frequent reoccurrence of drought events (Singh and Chudasama, 2020). The high temperatures and lowered rainfall alter temporal resource availability and biodiversity (Nkomo et al., 2006). In the past 40 years, arid and semi-arid regions have been shaped to be most vulnerable to climate change as a result of increased temperature and lowered rainfall, compared to other ecoregions (Nkomo et al., 2006; Huang et al., 2015; Singh and Chudasama, 2020; Fuller et al., 2021). The direct and indirect effects of increased temperatures and more variable rainfall alters the availability of food resources (Sarr, 2011; El-Bltagy and Madkour, 2012; Hetem et al., 2014). The physiology and behaviour of species will be impacted, influencing the distribution range of species, individual species welfare and species communities as a result of climate change (Fox et al., 1999; Root et al., 2003; Parmesan et al., 2000; Holmgren et al., 2006; Bellard et al., 2012; Rey et al., 2017; Fancourt et al., 2018).

1.2.1 Direct impacts of climate change

Changes in rainfall and temperature, and the occurrence of drought, have a significant impact on species and the productivity of species in an ecosystem (Fox et al., 1999; Conway, 2006; Rey et al., 2017). Rainfall is an essential factor for ecosystem production and ecosystem resources that mammals are dependent on (McNutt et al., 2019). Mammals may change in their phenology as a response to changing cues in the environment, which may then impact species population dynamics (Fox et al., 1999; Cunningham et al., 2015; Smit et al., 2016). The success of reproduction may be influenced by extreme environmental temperatures resulting from climate change (McNutt et al., 2019). Some species may employ physiological plasticity to cope with increasing heat and aridity, such as selective brain cooling or a change in diet, while others have morphological features like a light-coloured pelage to help adapt and cope

with climatic changes (Fuller et al., 2010). Other species may change their exposure to macroclimates by changing their active periods, distribution range or seeking suitable microclimates (Levy et al., 2019). Extinction or extirpation may result if species are unable to adapt to the effects of direct climate change (Fuller et al., 2010; Levy et al., 2019).

Rainfall plays an intrinsic role in supporting ecosystem biodiversity by supplying ecosystems and species with water (Chesson et al 2004; MacFadyen et al., 2018; Heffelfinger et al., 2018). Small events of rainfall in arid or semi-arid regions influence moisture in soils (Chesson et al., 2004), on which plants rely on for growth (Heffelfinger et al., 2018). Rainfall enables growth of plants and increases water content, nutrients and the biomass needed for sustaining mammals (Sala and Lauenroth, 2016; Heffelfinger et al., 2018). An increase in vegetation productivity induced by rainfall may decrease home ranges and the energy cost of mammals during foraging (Heffelfinger et al., 2018). Water is crucial for thermoregulation in the heat, and water loss in arid and semi-arid zone mammals is inhibited when mammals experience dehydration as a result of decreased water intake and decreased rainfall (Williams et al., 2001; Chesson et al., 2004; Fuller et al., 2016; Zhang et al., 2017; McKingley et al., 2018; Fuller et al., 2021).

Mammals will experience dehydration from evaporative water loss under heat stress when there is lack of water supply, especially in hot and dry arid or semi-arid regions (Fuller et al., 2016; Fuller et al., 2021; McKingley et al., 2018). An increase of water loss in mammals resulting from dehydration reduces evaporative cooling, resulting in an increase in core body temperature when exposed to heat (Hetem et al.,2014; Heffelfinger et al., 2018). In regions of low rainfall occurrence, preserving body water and water loss can be achieved in some mammals through selective brain cooling and an increase of the body temperature threshold for evaporative water loss, resulting in individuals sweating or panting later (Fuller et al., 2010; Fuller et al., 2014; Fuller et al., 2016; Strauss et al., 2017; Taylor, 1970). The Arabian oryx (*Oryx leucoryx*) conserves water and maintains homeostasis by using selective brain cooling during high temperature heat loads and by shifting its activity to the night and seeking shade during the day (Hetem et al., 2014). The Arabian oryx and Kangaroo rats also can minimize loss by concentration of urine volume and dry faeces (Walsberg et al., 2000; Fuller et al., 2016).

The morphology of an animal may also influence how the species responds to changes in the environment caused by climate change (Maloney and Dawson, 1994). An animal's pelage quality can influence the animal's heat gain (Dawson and Maloney, 2004; Fuller et al., 2010; Fuller et al., 2016). Coat colour and the thickness of fur may influence the extent to which radiation can penetrate through the fur to reach the skin (Fuller et al., 2010; Dawson and Maloney, 2014). Mammals with dark fur inhabiting hot environments absorb greater heat from solar radiation compared to mammals with a lighter coloured fur coat (Dawson and Maloney, 2008). Mammals with dark fur have a disadvantage in hot summers but possibly an advantage in cold winters (Dawson and Maloney, 2008; Fuller et al., 2016). The fur colour will however not be a determinate of preventing heat load if fur is thick (Dawson and Maloney, 2008). The decrease of fur thickness will have a stronger influence in altering heat load in mammals than the colour of fur in mammals (Dawson and Maloney, 2008).

To buffer the effects of climate change, some species may respond by altering their reproductive periods to improve reproductive success by inducing early birth or late birth to match environmental cues, ambient temperatures, and resource availability (Masters et al., 1998; McNutt et al., 2019). Excessive heat, however, can have direct effects on reproduction (McNutt et al., 2019). High body temperatures can result in decreased sperm potency and disturbance in the morphology of sperm (Fuller et al., 2016). Female species may experience disturbances in ovarian cells caused by heat, further impacting the development of a foetus (Fuller et al., 2016). In certain populations of African wild dogs (*Lycaon pictus*), reproductive success is greatest when environmental temperatures are low at the time of birth (McNutt et al., 2019). As temperatures increase, reproduction and rearing of African wild dog pups may decrease in success, impacting the survival of pups and African wild dog populations (McNutt et al., 2019). Meerkat pups in the Kalahari experience high air temperatures that increase water loss by evaporation, reducing diurnal body mass gain and affecting pup growth and survival (van de Ven et al., 2020).

Increased exposure to high temperatures when water is limited influences the increase of body temperature in mammals (Walsberg, 2000; Fuller et al., 2014; Levy et al., 2019). Often mammals will avoid the direct effect of increased air temperatures by seeking buffered microclimates (Levy et al., 2019; Fuller et al., 2014). However, during

high environmental temperatures, when there is limited spatial resources, competition for microclimates and predation increases, limiting activity and the ability of behavioural thermoregulation to buffer species (du Plessis et al., 2012). Mammals seek microclimates that provide cooler temperatures to decrease evaporative water loss and maintain homeostasis (McKinley et al., 2018; van de Ven et al., 2020; Fuller et al., 2021). Burrows, crevices, holes, and shade provide microclimates that aid in decreasing heat loads and limiting evaporative water loss in mammals (Fuller et al., 2014; Levy et al., 2019). However, large mammals have limited microclimates available for usage compared to smaller mammals (Fuller et al., 2016). When environmental temperatures are higher than the body temperature of small mammals, foraging would be limited or even ceased (du Plessis et al., 2012). Small mammals will either increase evaporative cooling or alternatively seek microclimates (du Plessis et al., 2012). Small mammals that use cooler microclimates such as burrows during hot periods can increases body water preservation and decreases hyperthermia (Walsberg, 2000; Fuller et al., 2021). The usage of microclimates decreases movement and decreases energy and water intake that would have been gained during foraging (Hetem et al., 2014; Fuller et al., 2016). Small mammals experience such rates of evaporative water loss during high temperatures and during periods of low water intake, which can further impact the foraging rates of small mammals (Walsberg, 2000; du Plessis et al., 2012). However, the usage of microclimates can potentially expose an animal to an increased risk of predation (Hetem et al., 2014; Fuller et al., 2016). Small mammals may still experience rates of evaporative water loss more than 5% of their body mass each hour, even when microclimates are used (du Plessis et al., 2012). Small mammals have a lower capacity for heat storage (van de Ven et al., 2020). Furthermore, small mammals will often increase of evaporative water loss as a result of energy needed for dissipating heat when panting (van de Ven et al., 2020). When environmental temperatures are high the golden spiny mouse (*Acomys russatus*) will decrease foraging and seek cooler microclimates to limit evaporative water loss (Levy et al., 2019). Aardvarks use burrows to decrease heat load (Weyer, 2018), while ground squirrels (*Marmotini sp*.) will often shuttle in and out of burrows to limit hyperthermia (Fick et al., 2009). Although seeking shade to avoid heat load will depend on body size, smaller mammals will gain heat load faster than larger mammals (Fuller et al., 2014; Fuller et al., 2016). The usage of shade may not always be sufficient to decrease body temperature (Schmidt-Nielsen et al., 1957). Dehydrated camels (*Camelus sp.*) using shade during summer still experience an increase of core

body temperature (Schmidt-Nielsen et al., 1957; Bekele et al., 2013). Bigger mammals such as elephants (*Loxodontus africana and Elephas sp.)* also seek shade and experience a slower rate of increase of core body temperature especially when water resources are available (Mole et al., 2016). The decrease or lack of microclimates resulting from habitat destruction or degradation will increase mammal vulnerability to climate change, impacting the ability of large mammals to decrease core temperatures through behavioural thermoregulation, further limiting species' ability to buffer through climate change unless species are able to change active periods (Fuller et al., 2014; Levy et al., 2019).

High environmental temperatures can increase heat stress and heat load in mammals (Fuller et al., 2016), leading mammals to change active periods (Moyer-Horner et al., 2015; Levy et al., 2019). Change in time of activity from diurnal to crepuscular or nocturnal is often linked to seeking cooler environmental temperatures. The change of active periods also permits mammals to avoid high water loss during the day (Walsberg, 2000; Williams et al., 2001; Fuller et al., 2016; McKinley et al., 2018; Levy et al., 2019). Species such as pikas (*Ochotona sp.)* shorten active periods during the day to limit heat load when temperatures are high (Moyer-Horner et al., 2015). Levy et al. (2019) has demonstrated the behavioural process in which mammals shift active periods shown in Figure 1.1. Nocturnal species make use of cooler evening conditions which aids in limiting the potential of overheating and water loss (McNutt et al., 2019; Levy et al., 2019). Being active at night, however, requires energy to defend body temperature. Aardvarks changed their active periods from nocturnal to diurnal after drought, as a result of the high energy requirements to sustain body temperatures at night (Weyer et al., 2020). Foraging time of aardvarks also decreased during periods of drought (Weyer et al., 2020). The occurrence of drought impacted the survival of populations of the aardvark by reducing total energy and water intake (Weyer et al., 2020). The Arabian oryx gained supplementary water when consuming plants with high water content at night (Williams et al., 2001; Fuller et al., 2016). Furthermore, it was able to reduce its diurnal activity and shift activity to the night without compromising its total daily activity time (Hetem et al., 2012). Nocturnal activity may not limit exposure to high temperatures during warmer months, so foraging during high night temperatures will further impact the body water needed for thermoregulatory needs (Walsberg, 2000).

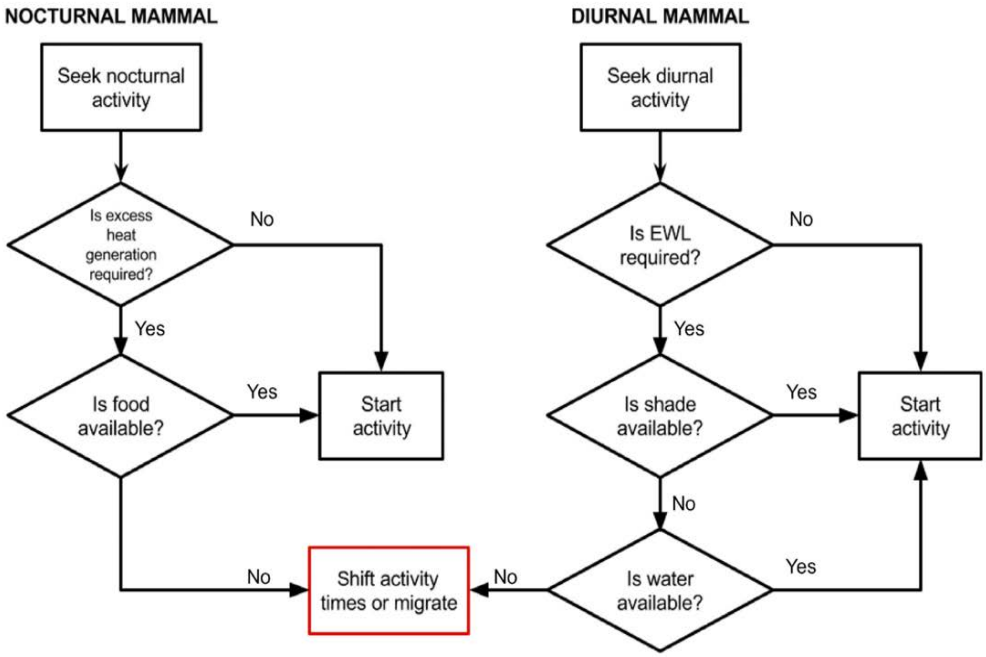


Figure 1.1: How energy and water demand, influence nocturnal and diurnal animals to change their activity periods. From Levy et al. 2019.

1.2.2 Indirect impacts of climate change

Increasing temperatures and decreasing rainfall are factors that lead to indirect impacts of climate change (Cahill et al., 2013), for example by changing the availability of food resources or changing trophic interactions (Stange and Ayres, 2010). Drought occurrence is increasing with climate change, impacting moisture, food resource availability, the distribution range of species, competition, and resulting in shifts in trophic levels in an ecosystem (Fox et al., 1999; Holmgren et al., 2006). A decrease in rainfall particularly affects species in arid and semi-arid regions that rely on already-short periods of rainfall for productivity (Parmesan et al., 2000; Holmgren et al., 2006). A reduction in food availability influences the population dynamics of both predator and prey species, leading to potential declines of population size and changes in distribution ranges (McNutt et al., 2019). Decreased food availability in arid areas influences energy gain in mammals, influencing body temperatures, metabolic rates, and maintenance of visceral organs (Fuller et al., 2010). When arid ecosystems have sufficient food supply during dry winters, many mammals can maintain core body temperatures through sufficient energy intake and water intake via food (Fuller et al., 2016).

Species' responses to indirect effects of climatic change may include a change in their diet to reduce the energy cost during foraging when their usual food resources are limited (Jumbam et al., 2019). The change in diet in some species is best achieved when species can disperse into areas that are suited for their physiological adaption to climatic vulnerability (McNutt et al., 2019). As droughts are predicted to increase in frequency, vegetation may decrease and predator species will be affected, resulting from fluctuations of prey population sizes. The stability of ecosystems may be impacted as a result of predator and prey population fluctuations (Rey et al., 2017). Some temperate-zone mammals such as the red deer (*Cervus elaphus)* respond to decreased food supply by reducing the size of visceral organs and improving nutrient extraction gained when consuming food (Fuller et al., 2016). The Arabian oryx in an arid zone would decreases visceral organ mass to reduce metabolic rate during decreased food and water resources (Ostrowski et al., 2006; Fuller et al., 2016). The lower metabolism when resources are limited reduces body mass loss (Ostrowski et al., 2006).

Herbaceous vegetation will depend on the occurrence of rain to germinate, grow, and produce seeds (Holmgren et al., 2006). Insects are very responsive to changes in climate (Stange and Ayres, 2010). Climate change can have an impact on insect species' population and insect predators due to vegetation degradation caused by the indirect impacts of climate change (Stange and Ayres, 2010). Insects are considered to have an intrinsic role in ecosystems (Ayieko et al., 2010). Depending on the geographic location, insect populations may thrive or decline as an effect of climate change (Ayieko et al., 2010; Weyer, 2018). Drought has a significant impact on the population abundance of insects by affecting the physiology of insects (Masters et al., 1998). The biomass of invertebrates is likely to be altered by hotter and drier conditions, with a crash of ants and termite population species occurring during drought conditions (Nel and Hewitt, 1969). Savanna ecosystems of the Kalahari are being impacted by climate change and altered land-use (Tews et al., 2004). The effects of altered land-use and climate change in the Kalahari savannah ecosystem, influences species diversity, especially that of small ground-dweller mammals (Tews et al., 2004). It is believed that animals that have a generalist diet and feed on a variety of food items will be better off than an animal like the aardvark that is a specialist feeder (Rey et al., 2017).

Generalist feeders have a wider range of habitat and diet compared to specialist feeders (Smith and Reeves, 2012; Jumbam et al., 2019). Generalist species are most likely to be buffered when preferred food availability or prey populations are limited (Jumbam et al., 2019; Roberts and Stewart, 2018). Specialist species are likely to be pushed to alter their behaviour to gain energy requirements under climate change or to become extinct when energy requirements are not met (Melillo et al., 2011). The Arctic fox *(Canis lupis arctos)* can thrive amidst limited food resources by feeding in a variety of food webs (Dalerum et al., 2012). However, increasing climate change impacts may challenge the ecological resilience of generalist species too (Smith and Reeves, 2012). The ability to change between food webs may not be possible for specialist species (Dalerum et al., 2012). As climate influences the occurrence of rainfall, specialist species populations are more likely to decline (Jumbam et al., 2019). For specialist species, habitat range and diet may be narrow compared to generalist species (Shilereyo et al., 2019). Therefore, for specialist species to thrive, ecosystems should be maintained by protecting and preserving vegetation and water supply to allow access to preferred prey (Shilereyo et al., 2019).

1.3 Potential effects of climate change in Africa on bat-eared foxes

1.3.1 General ecology of bat-eared foxes.

Bat-eared foxes (*Otocyon megalotis*) are small mammals with body sizes ranging from 3.0 kg to 5.3 kg. Bat-eared foxes are distinguished by their large ears that are used to detect sound made by their preferred insect prey (Malcom, 1986; Nel, 1990; Grant and Samways, 2015). The bat-eared fox is part of the Canidae family and is the only member of the *Otocyon* genus (Westbury et al., 2017). Bat-eared foxes have a pale yellow-brown colour and have a relatively long black- brown tail and short legs (Figures 1.2 and 1.3; Clark, 2005; Grant and Samways, 2015).



Figure 1.2: Two bat-eared foxes captured during a period of foraging in the winter season at Tswalu Kalahari Reserve (Photo credit: Letsema Molete).



Figure 1.3: Three bat-eared foxes captured during a resting activity in the winter at Tswalu Kalahari Reserve (Photo credit: Letsema Molete)

Bat-eared foxes are found in semi-arid regions of eastern and southern Africa (Lamprecht, 1979; Figure 1.4). They have a distribution range in southern Africa that extends mainly across Angola, Namibia, Botswana, Mozambique, and South Africa, while in the east African distribution range extends across Ethiopia, South Sudan Kenya, and Tanzania (Coetzee, 1977; Kingdon, 1988; Malcom, 1986; Pauw, 2000; Clark, 2005). In South Africa, bat-eared foxes can be found in the arid regions of the North-West, Western Cape, Northern Cape, Limpopo, Free State, Eastern Cape, and Gauteng provinces, but they are absent in Kwa-Zulu Natal, as well as in neighbouring countries, Lesotho and Eswatini (Kok and Nel, 1992; Skinner and Chimimba, 2005, Clark, 2005; Nel and Maas, 2013; Figure 1.5). The home range of bat-eared foxes can range between 0.3 km^2 and 2.0 km^2 (Lamprecht, 1979; Clark, 2005), however, often changes during the different seasons of the year (Clark, 2005). Their distribution range coincides with the distribution and abundance of their most consumed prey, harvester termites (Nel, 1990; Clark, 2005; Grant and Samways, 2015). Périquet and le Roux (2017) also highlighted that the home range of bat-eared foxes in the Kalahari is driven by the consistent abundance of prey species, irrespective of habitat type.

Bat-eared foxes use habitats that vary, from dry open plains, low shrub grasslands, short grassland, karoo scrub and open woodland (Kuntzsch and Nel, 1992; Mackie and Nel, 1989). Bat-eared foxes will often make use of vegetation that is tall and thick for cover (Smithers, 1971; Kuntzsch and Nel, 1992; Mackie and Nel, 1989). Insects that bat-eared foxes consume depend on grass productivity for growth (Berry, 1981; Périquet and le Roux, 2017). Bat-eared foxes will use similar habitat as insects that they consume, which often coincides with the close ecological needs between insect species and bat-eared foxes (Berry, 1981; Mackie and Nel, 1989; Mackie, 1990; Périquet and le Roux, 2017). Predator avoidance, insect abundance, den site selection and seasonality are other factors that influence the selection of habitat by bat-eared foxes (Maas and Macdonald 2004; Periquet and le Roux, 2017).

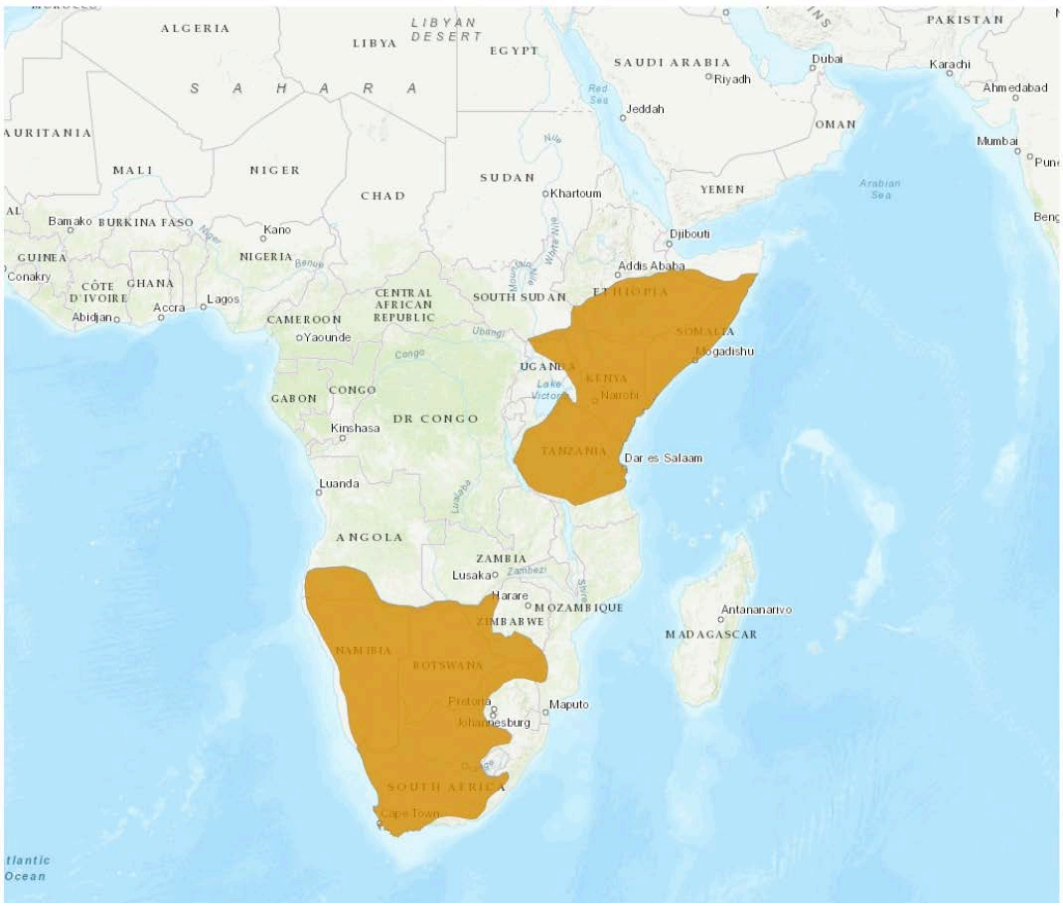


Figure 1.4: Population distribution range (highlighted area) of bat-eared fox sub-species in east (*Otocyon megalotis virgatus)* and southern Africa (*Otocyon megalotis megalotis*) (IUCN, 2021)

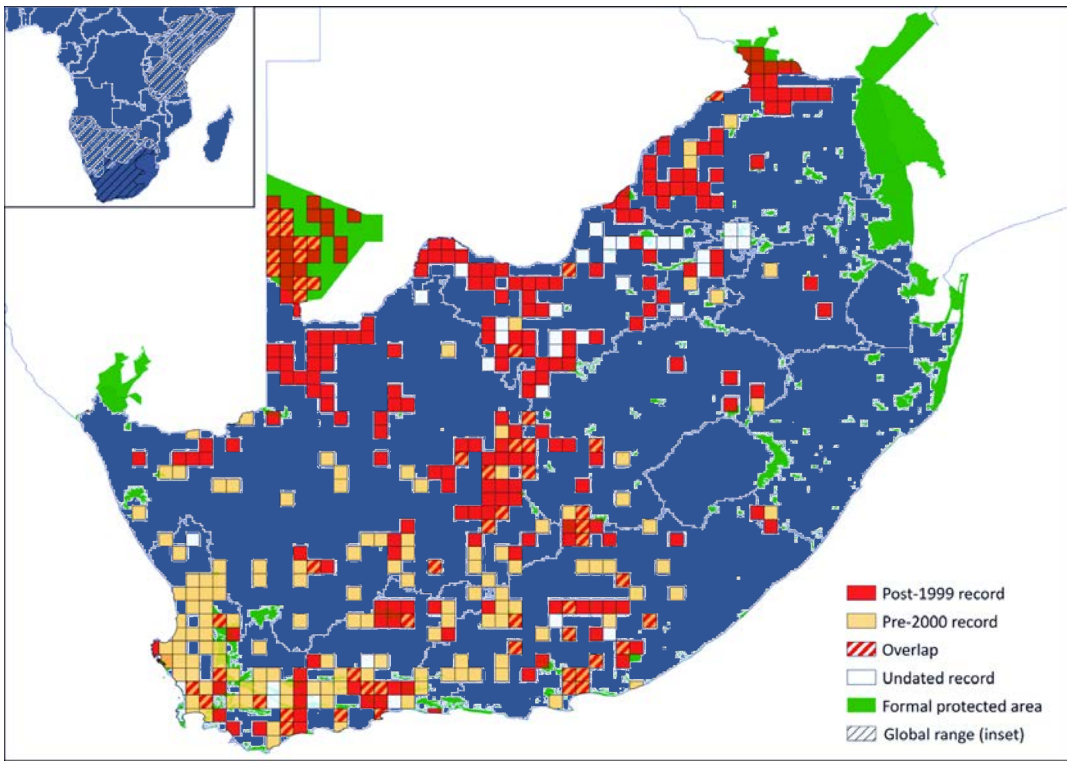


Figure 1.5: Distribution of bat-eared foxes in South Africa, prior to the year 2000 and after, as per the Red List of Mammals of South Africa (Dalerum et al., 2016).

Bat-eared foxes are often found living in pairs or groups (Lourens and Nel, 1990; Figures 1.2 and 1.3). The bonding and mating of the monogamous bat-eared foxes occurs during the late winter and early summer (Clark, 2005). Sexual maturity of bat-eared foxes takes place during the eighth and ninth month of their growth (Clark, 2005). The breeding season of bat-eared foxes often corresponds with periods of rainfall (Clark, 2005). The gestation period takes 60 to 75 days, producing a litter of up to six pups (Clark, 2005; Wright et al., 2010; Figure 1.6). Females are known for having longer feeding periods than males in summer to meet the demands of lactation that ranges from 14 to 15 weeks (Lamprecht, 1979; Lourens and Nel, 1990). Pups will often appear near the beginning of the wet season in South Africa, between September and December (Nel, 1984; Clark, 2005). Males will spend time to guide, groom and defend pups against predators (Nel 1990; Pauw, 2000; Wright, 2006). Pups will then disperse from the group at the age of five to six months (Lamprecht, 1979).



Figure 1.6: Bat-eared fox pups emerging from their den at Tswalu Kalahari Reserve. (Photo credit: Wendy Panaino)

The bat-eared fox is a species that provides ecosystem services by influencing the structure of vegetation when digging for prey and through intake of that prey. Bat-eared foxes influence the dynamics of disease in an ecosystem by being a vector to several viruses. Bat-eared foxes can develop and spread rabies, canine distemper, and canine parvovirus as well as the parasite *Trichinella nelson* (Pozio et al., 1997; Courtin et al., 2000; East et al., 2001; Bengis et al., 2002; Van de Bilt et al., 2002; Dalerum et al 2016). Rabies outbreaks are becoming more apparent in southern Africa (Sabeta et al., 2007), with the increase in disease spread coinciding with a decrease of insect prey abundance (Ginsberg and Macdonald, 1990; Nel, 1993). The possibility of rabies spreading increases when contact between populations of bat-eared foxes occurs or population of bat-eared foxes is in contact with other mammal species (Nel, 1993). The increase of rabies within a geographic area may further impact population densities in a region (Nel, 1993).

Bat-eared fox populations, however, are relatively stable. Therefore, bat-eared foxes are considered Least Concern on the Regional Red List, National Red List status and the Global Red List status (Dalerum et al., 2016). The Threatened or Protected Species regulations have considered the species as protected. The Convention on International Trade in Endangered Species has not listed the bat-eared fox (Nel and Maas, 2004).

Whether climate change poses a significant extinction threat to bat-eared foxes is not yet known (Dalerum et al., 2016).

1.3.2 Diet of bat-eared foxes

Bat-eared foxes are the only Canidae member in southern Africa that eats mainly insects, with harvester termites being their most consumed prey (Lamprecht, 1979; Kuntzsch and Nel, 1992). The foxes are known for using their well-adapted large ears for detecting sounds made by insect prey. The usage of their ears to detect prey does not necessarily lead to feeding on all insect prey, but rather on the preferred insect prey (Grant et al., 2015). Prey sources also include ants (Hymenoptera), spiders (Arachnida), grasshoppers (Orthoptera), scorpions (Scorpiones), plant material (mainly wild berries and seeds), beetles (Coleoptera) and their larvae (Mackie and Nel, 1989; Kok and Nel, 1992; Kuntzsch and Nel, 1992; Jumbam et al., 2019).

Previous studies have examined the diet of bat-eared foxes using various methods, which include examining stomach contents (Berry 1981; Kok and Nel, 1992;), scat collection (Nel, 1990; Kuntzsch and Nel, 1992; Stuart et al., 2003; Klare et al., 2011; Grant and Samways, 2014) and observations of feeding (Jumbam et al., 2019). One study used both scat collection and observations of feeding (Koop and Velimirov, 1982) while another used both scats and stomach content assessment (Malcom, 1986).

Despite different methods being used, the content in diet was found to be broadly similar. The studies show that the preferred dietary source, Isoptera, was consumed throughout the year, with Hymenoptera and Coleoptera as the second and third preferences. The content of consumed prey species varied seasonally. Seasonality appears to alter the quantity of Isoptera in the diet of bat-eared foxes. Previous studies have shown that the diet during winter and autumn had the highest quantities of Isoptera (Kok and Nel, 1992; Stuart et al., 2003; Klare et al., 2011; Jumbam et al., 2019) and Coleoptera as the second-most consumed invertebrate prey (Stuart et al., 2003). In other studies, Isoptera and Hymenoptera were consumed more in the dry season, while Coleoptera were consumed more in the summer. Kuntzsch and Nel (1992) argued that although bat-eared foxes consumed Isoptera, the preferred content during winter were berries. During spring and summer, the presence of other invertebrates such as Arachnida and Scorpiones in the diet increased, as well as

berries and seeds. Seasonality influenced the diet of bat-eared foxes especially when preferred prey species were not available (Kuntzsch and Nel, 1992). When termite prey was low in quantity, bat-eared foxes not only consumed other invertebrates and plants but expanded their diet to include mammals and reptiles (Stuart et al., 2003). Rainfall has shown to influence the consumption of prey species seasonally (Berry, 1981; Jumbam et al., 2019). The consumption of reptiles and mammals is thought to be an opportunistic behavioural trait of the bat-eared foxes (Berry, 1981), with the presence of species like snakes, lizards, and mice, as well as frogs and bird nestlings (Berry, 1981; Kok and Nel, 1992; Jumbam et al., 2019).

In other studies, seasonal changes in diet were not investigated, however Isoptera was consumed throughout the year. The occurrence of Coleoptera was the second-most consumed invertebrate along with the presence of seeds and grass were also present in the diet (Koop and Velimirov, 1982; Kuntzsch and Nel, 1992; Stuart et al., 2003). Berry (1981) highlighted plants as the second-most consumed and Coleoptera were less preferred throughout the year compared to other studies. Although the preferred prey was consumed throughout the year, the abundance of content was based on the availability of food resources during different seasons and on limitations of energy costs when foraging (Kuntzsch and Nel, 1992; Stuart et al., 2003).

A summary of the diet of bat-eared foxes recorded across different locations in southern African and east Africa is shown in Table 1.1. Studies conducted in the Northern Cape revealed that 16% to 70% of the bat-eared fox diet consists of Isoptera (Kok and Nel, 1992; Stuart et al., 2003; Klare et al., 2011; Jumbam et al., 2019). Isoptera were consumed regardless of their availability in the environment (Kok and Nel, 1992; Stuart et al., 2003; Jumbam et al., 2019). Hymenoptera or Coleoptera were usually the second most common invertebrate in the diet (Stuart et al., 2003; Klare et al., 2011; Jumbam et al., 2019). A study that was conducted in the Northern Cape and Free-State found that Coleoptera (21%) were more common in the diet than Isoptera (16%) (Kok and Nel, 1992). In Botswana, an area with similar climatic conditions to the Northern Cape, Isoptera made up much of the diet (89%), while Coleoptera (6%) were the only other invertebrate present (Koop and Velimirov, 1982). In the Western Cape, Isoptera comprised of 22% to 32% in the bat-eared fox diet. Coleoptera was the second-most consumed invertebrate (Kuntzsch and Nel, 1992; Stuart et al., 2003; Grant and Samways, 2014). Plants formed 9% to 24% of the diet of bat-eared foxes in

the Western Cape and were consumed more in comparison to Hymenoptera (3% to 16%). In Limpopo, a study showed that 44% consisted as Isoptera in the diet of bat-eared foxes and plants contributed 42% more compared to Coleoptera (11%) (Berry, 1981). In Kenya and Tanzania (Malcom, 1986), plants did not contribute to the diet of bat-eared foxes, although the overall diet mirrors a similar diet contribution as the southern African studies. Overall, Coleoptera and Isoptera were the food item most found in the diet of bat-eared foxes at all sites.

The consumption of other invertebrate species formed a smaller proportion of the bat-eared fox diet and varied depending on geographic location. Lepidoptera was recorded in two studies, in the Northern Cape and Free State. The studies revealed that the representation of Lepidoptera in bat-eared fox diets can range from ~0.9% (Jumbam et al., 2019) to ~10% (Kok and Nel, 1992). Orthoptera was recorded in six studies across the Northern Cape and Western cape. At four of the sites, two in the Northern Cape and two in the Western Cape, Orthoptera consisted as ~1% to 5% of the diet of bat-eared foxes (Stuart et al., 2003; Klare et al., 2011; Grant and Samways, 2014; Jumbam et al., 2019). In the Free State, Northern Cape and Western Cape Orthoptera formed ~10 % to 21% of the bat-eared foxes' diet (Kok and Nel, 1992; Kuntzsch and Nel, 1992). Diplopoda was recorded in two studies, in which one study was solely in the Northern Cape and another in the Free State and Northern Cape showed that ~0.03% to 1% comprised of Diplopoda in the diet of bat-eared foxes (Kok and Nel, 1992; Jumbam et al., 2019). Mantodea was recorded in one study in the Northern Cape. The study showed that ~ 0.06% consisted of Mantodea in the diet of bat-eared foxes (Jumbam et al., 2019). In three studies conducted across three different geographical location, Limpopo, Northern Cape, and Western Cape showed that ~0.7% to 3% consisted of Arachnida in the diet of bat-eared foxes (Berry, 1981; Kok and Nel, 1992; Stuart et al., 2003; Jumbam et al., 2019).

Table 1.1: Compilation of previous studies on the diet of bat-eared foxes in various habitats (Kalahari, Savanna, Grassland, Fynbos and Karoo), using different study methods. Species are expressed as scats relative percentage occurrence approximating to 100%. Table adapted from Jumbam et al., 2019.

Authors	Jumbam et al., 2019	Klare et al., 2011	Kok and Nel, 1992	Stuart et al., 2003	Grant and Samways, 2014	Kuntzsch and Nel, 1992	Koop and Velimirov, 1982	Berry, 1981	Malcom, 1986
Geographical location and habitat	Northern Cape, Kalahari	Northern Cape, Karoo	Free State and Northern Cape	Western Cape	Western Cape, Karoo and fynbos	Western Cape, Karoo	Maun, Kalahari	Limpopo, Savanna	Kenya and Tanzania, Grassland
Method of study	Observations	Scat collection	Stomach content	Scat collection	Scat collection	Scat collection	Observations and scat collection	Stomach content	Scat collection and stomach content
Hymenoptera	8	20	12	15	3	14	-	-	16
Coleoptera	11	8	21	32	40	24	6	11	23
Lepidoptera	0.9	-	10	-	-	-	-	-	-
Orthoptera	5	5	10	1	3	21	-	-	-
Isoptera	70	28	16	32	22	24	89	44	61
Diplopoda	0.03	-	1	-	-	-	-	-	-
Mantodea	0.06	-	-	-	-	-	-	-	-
Hemiptera	1	-	-	-	-	-	-	-	-
Neuroptera	2	-	-	-	-	-	-	-	-
Scorpiones	0.2	4	5	5	-	-	-	-	-
Arachnida	0.7	-	-	1	-	-	-	3	-
Reptilia	0.1	1	2	1	2	-	-	0.1	-
Mammalia	0.2	5	5	4	6	-	-	-	-

Plants, seeds and other	0.8	29	18	9	24	17	5	41.9	-

Within Isoptera, *Hodotermes mossambicus* has been noted as the most consumed prey item by bat-eared foxes in various studies, and particularly in the Northern Cape (Table 1.2; Berry, 1981; Koop and Velimirov, 1982; Bothma et al., 1984; Nel, 1990; Kuntzsch and Nel, 1992; Kok and Nel, 1992; Stuart et al., 2003; Klare et al., 2011; Jumbam et al., 2019). Other Isoptera species in the diet of bat-eared foxes as shown include *Trinervitermes trinervoides*, *Odontotermes* species and *Amitermes* species (Table1.2; Malcom, 1986; Kok and Nel, 1992; Stuart et al., 2003; Klare et al., 2011; Grant and Samways, 2014).

Although the availability of *T. trinervoides* in the Northern Cape was high, the species contributed only 0.1% to the diet of bat-eared foxes (Klare et al., 2011). Stuart et al., (2003) found that although *T. trinervoides* were present in the diet of bat-eared foxes in the Western Cape, the quantity was low, forming 1% of the overall diet. Contrary to other studies, *T, trinervoides* were present in relatively high numbers (6%) in the diet of bat-eared foxes in Namibia (Bothma et al., 1984). The low occurrence of *T. trinervoides* in the diet of most bat-eared foxes may be a result of low tolerance to chemicals released from the termites, that contain diterpenes and pinene (Braekman et al., 1984; Richardson and Levitan, 1994). The kidneys, intestines and nervous system may be affected when diterpenes and pinene are consumed by species that are not well adapted to consume prey that contain these chemicals (Richardson and Levitan, 1994). *Odontotermes* along with *Amitermes* were both consumed in the Northern Cape, although they formed less than 1% of the diet (Kok and Nel, 1992). In contrast, *Odontotermes* made up 61% of the overall diet in Kenya and Tanzania and were the only termites consumed by bat-eared foxes there (Malcom, 1986). In the Western Cape, *Amitermes* were present in the diet of bat-eared foxes, forming 22% of the overall diet (Grant and Samways, 2014). *Microhodotermes viator* have been noted as termites that are also consumed by bat-eared foxes (Kuntzsch and Nel, 1992), however the reviewed diet studies did not consist of these termite species.

Table 1.2: Compilation of previous studies on the occurrence of Isoptera species in the diet of bat-eared foxes across various habitats (Kalahari, Savanna, Fynbos and Karoo).

Authors	Jumbam et al., 2019	Klare et al., 2011	Kok and Nel, 1992	Stuart et al., 2003	Grant and Samways, 2014	Kuntzsch and Nel, 1992	Koop and Velimirov, 1982	Berry, 1981	Malcom, 1986	Bothma et al., 1984
Geographical location and habitat	Northern Cape, Kalahari	Northern Cape, Nama karoo	Free State and Northern Cape	Western Cape, Karoo and fynbos	Western Cape, Karoo and fynbos	Western Cape, Karoo	Maun, Kalahari	Limpopo, Savanna	Kenya and Tanzania, Grassland	Namibia, Shrub grassland
Hodotermes mossambicus	70	28	16	32	-	24	89	44	-	17
Trinervitermes trinervoides	-	0.1	0.5	1	-	-	-	-	-	6
Odontotermes	-	-	0.5	-	-	-	-	-	61	-
Amitermes	-	-	-	-	22	-	-	-	-	-

1.3.3 Potential effects of climate change on the preferred dietary item of bat-eared foxes, termites

Temperature, rainfall, relative humidity, and solar radiation are climatic variables that impact the survival of insect populations (Stange and Ayres, 2010). Temperature has an influence on insect fitness and survival by increasing water loss and increasing body temperature, impacting the temperature tolerance and sensitivity that enables insects to forage (Mitchell et al., 1993; Stange and Ayres, 2010). The thermal sensitivity (Q10) of insects will rely on temperature parameters (Nespolo et al., 2003). Metabolic rates in insects are impacted by ambient temperature and body mass of insects (Nespolo et al., 2003). The Q10 effect at high temperatures and low temperatures will influence dispersal and reproduction of insects (Prestwich and Walker, 1981, Rogowitz and Chapell, 2000, Tattersall et al., 2012). Loss of water particularly impacts insects that cut and transport grass to colonies, like termites (Mitchell et al., 1993; Inder, 2013). Drought, which is occurring more frequently with climate change in drylands (Mirzabaev et al., 2019), reduces long-term soil moisture and food (vegetation) availability for insect species (Weyer, 2018). The occurrence of drought often leads to a decrease of insect species populations and species that depend on insects as food resources (Nel and Hewitt, 1969; Masters et al., 1998; Inder, 2013; Weyer, 2018). However, an occurrence of rainfall can improve vegetation growth and insect population and productivity (Masters et al., 1998). Ants and termites are insect species that depend heavily on rainfall for survival, and often form large portions of the diet for bat-eared foxes when available (McNab, 1984; Ayieko et al., 2010; Taylor et al., 2018). They likely provide not only energy but also water to bat-eared foxes, as shown for other myrmecophagous species (Weyer, 2018; W. Panaino, unpublished observations). Ecological changes in an ecosystem are often seen through monitoring of insects and other invertebrates (Sharma, 2010). Understanding the effects of climate change on myrmecophagous species and insect populations is, therefore, essential for understanding the interaction between species at different trophic levels, and the management and monitoring of ecosystems.

Harvester termites (*Hodotermes mossambicus*) are insects that harvest grass but often prefer dryland areas that are low in rainfall (Nel and Hewitt, 1969; Duncan and

Hewitt, 1989; Inder, 2013). *H. mossambicus* actively forages above-ground and builds its colony approximately 6 m underground (Heidecker and Leuthold, 1983; Inder, 2013). The colony is made up of adult workers, larvae, soldiers, and castes (Duncan and Hewitt, 1989; Inder, 2013). The adult workers are divided into two categories; minor and major, while the larvae are categorised as small and large in the colony (Nel et al., 1986; Duncan and Hewitt, 1989; Mitchell et al., 1993). In colonies of *H. mossambicus* there are pigmented major and minor workers that experience temperature tolerance differently. Temperature tolerance of both minor and major pigmented termite workers is higher than that of the unpigmented larvae (Nel and Hewitt, 1969; Mitchell et al., 1993). Large larvae may carry out work done by the adult workers at critical temperature limits as adult workers are more susceptible to water loss than large larvae (Nel et al., 1969). *H. mossambicus* depends on grass, and often harvest dry grass during autumn and winter, requiring the termite species to be most active during these two seasons (Nel and Hewitt, 1969; Mitchell et al., 1993). Termite population richness typically increases in moist regions (Davis et al., 1998; Ayieko et al., 2010). Increased temperature and decreased rainfall affect the moisture of soil and impacts the growth of vegetation which *H. mossambicus* depends on, limiting their populations (Nel and Hewitt, 1969a; Nel and Hewitt, 1969b; Ayieko et al., 2010; Taylor et al., 2018).

1.3.4 Activity patterns of bat-eared foxes linked to diet

Bat-eared foxes have been observed being active and foraging during diurnal and nocturnal periods (Koop and Velimirov, 1982; Klare et al., 2011; Jumbam et al., 2019). The activity periods of bat-eared foxes depend on season, temperature, and availability of food resources (Koop and Velimirov, 1982). The influence of rainfall and environmental temperatures impacts the seasonal quantity of prey species, as a result bat-eared foxes change active periods to meet energy requirements from prey, consequently changing the seasonal diet of bat-eared foxes (Masters et al., 1998; Périquet and le Roux, 2017; Jumbam et al., 2019). In southern Africa, the timing of foraging periods of bat-eared foxes depends on the active periods of insect prey, availability of insect prey and season (Klare et al., 2011; Jumbam et al., 2019). During cold winters, diurnal foraging mainly occurs, often extending into nocturnal foraging

(Nel, 1990). During summer, bat-eared foxes exhibit diurnal active periods of foraging and resting periods during the night (Nel, 1978; Lourens and Nel, 1990). Summer foraging may occur during the night extending into the early hours of the morning (Nel, 1978; Lourens and Nel, 1990; Nel, 1990; Koop and Velimirov, 1982). Bat-eared foxes likely alter their active period not only for optimal food intake, but also to increase energy intake from prey when foraging, especially when their preferred prey is limited (Koop and Velimirov, 1982; Lourens and Nel, 1990).

1.4 Dissertation aims

The purpose of my study is to gain a proximate understanding of the responses of bat-eared foxes to changes in an arid environment by investigating what they feed on, in an arid Kalahari environment. Specifically, I investigated the seasonal diet and activity periods of bat-eared foxes in response to changes in environmental conditions over one year.

I started my study when long-term monitoring of invertebrates (as part of the Kalahari Endangered Ecosystem Project) had revealed that ant and termite numbers were unusually low, as shown in Figure 1.7. The data were obtained only using pitfall traps, which likely underestimate the availability of subterranean species (Greenslade and Greenslade, 1971; Greenslade, 1973), particular in termites. However, observations and measurements on two other myrmecophagous mammals, the pangolin and aardvark, at the same study area indicated that these animals had insufficient food availability (W. Panaino and M. Phakoago, unpublished observations). Aardvarks, which feed preferentially on *H. mossambicus* (Weyer, 2018), a prey also consumed by the bat-eared foxes, were observed to be in very poor body condition, most likely reflecting starvation (Figure 1.8). I therefore aimed to assess whether bat-eared foxes also were likely to be nutritionally compromised through low ant and termite numbers, or whether they were able to cope through the intake of other prey items.

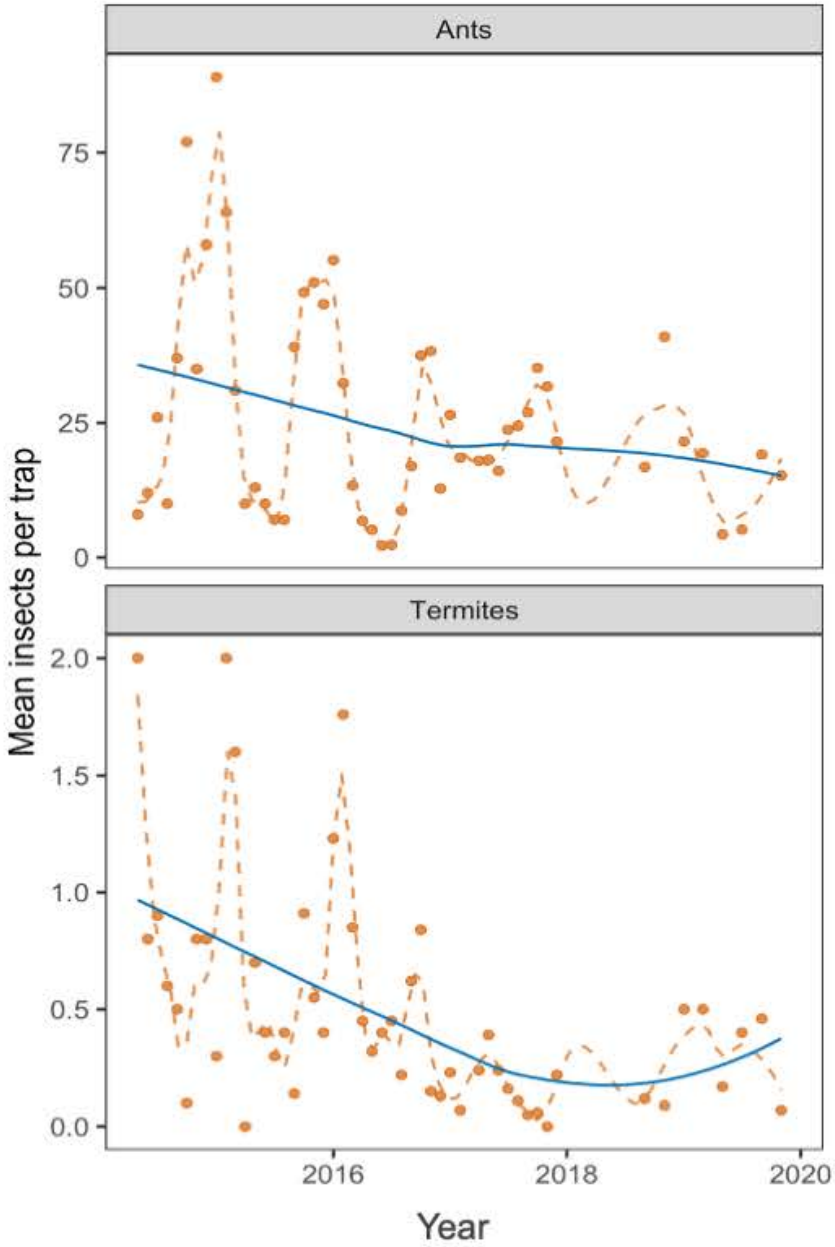


Figure 1.7: Mean number of in ants (top) and termites (bottom) caught in pitfall traps as part of a long-term monitoring of insects at Tswalu Kalahari Reserve (unpublished data, Kalahari Endangered Ecosystem Project). The fitted curves show the seasonal fluctuations and prey abundance trends (blue line), with insect numbers usually highest around the time of highest summer rainfall.



Figure 1.8: Aardvark in poor body condition at my study site (Tswalu Kalahari Reserve) in June 2019 (during my study period of bat-eared foxes). (Photo credit: Wendy Panaino)

I investigated variations in weather using miniature data loggers to measure black globe (environmental) temperature and rainfall occurrence using rainfall gauges. I assessed how grass cover impacts insect invertebrate prey seasonally. I quantified prey availability using pitfall traps every second month. I investigated the nutritional ecology of bat-eared foxes by assessing their dietary intake using scats. I investigated the activity periods of bat-eared foxes by recording the times when bat-eared foxes across the study site were observed to be active.

I hypothesized that bat-eared foxes would eat alternative species if harvester termites were not readily available, as indicated by the long-term monitoring and pitfall traps during my study period. I also hypothesized that the intake of the highly utilized prey (harvester termite, *H. mossambicus*) would vary seasonally, with foxes having a greater prey species variety in winter compared to in summer. As shown previously (Koop and Velimirov, 1982; Lourens and Nel, 1990; Périquet and le Roux, 2017; Levy et al., 2019), I expected that the active periods of the foxes would vary seasonally,

with the foxes having more diurnal periods of activity in winter compared to in summer (more active nocturnally).

CHAPTER 2

METHODS AND MATERIALS

2.1. Study area

I conducted fieldwork for this study at Tswalu Kalahari Reserve (Tswalu) from March 2019 to March 2020. Tswalu is a game reserve of 110 000 ha located in the Northern Cape, South Africa (S27˚ 14’57.50” E22º 22’52.00”) (Figure 2.1). Tswalu is situated in an arid environment. Annual rainfall in Tswalu ranged from 99 mm to 375 mm over the years of 2015 to 2020, with mean rainfall of 228 mm during that period. Tswalu consists of sandy savannah biome and dune bushveld along the quartzitic Korannaberg mountains (Davis et al., 2010), where the mountain lies in a transitional zone of two ecotypes: Kalahari dune and arid savannah. Tswalu consists of three fenced areas (Figure 2.2): a predator camp that includes lions, a roan and sable breeding camp, and the lion exclusion area (Tokura et al., 2018).



Figure 2.1: Geographical location of Tswalu Kalahari Reserve in South Africa (Google Earth, 2021)

The lion and lion-exclusion areas contain a wide variety of mammals. Myrmecophagous mammals occur at Tswalu, including bat-eared foxes *(Otocyon megalotis)*, ground pangolins *(Smutsia temminckii),* aardvark *(Orycteropus afer)* and aardwolf *(Proteles cristata).* Bat-eared foxes occur in all the sections of the reserve. However, I conducted the study in the lion-exclusion area, further specified in section 2.2.

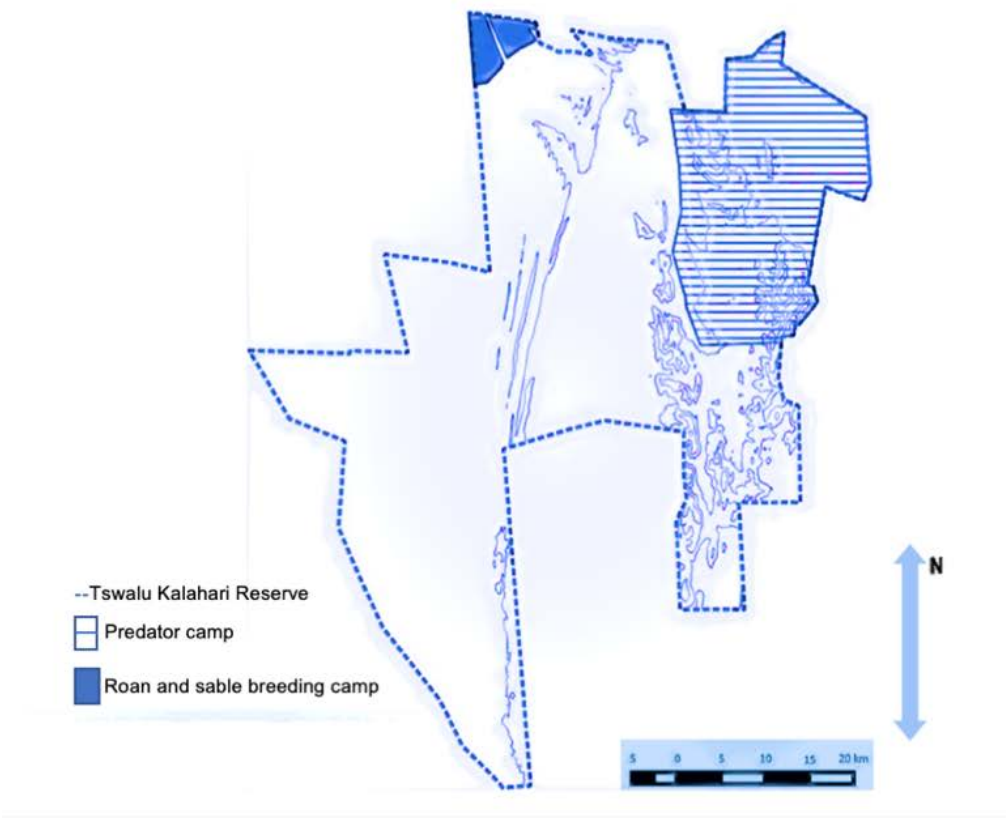


Figure 2.2: Tswalu Kalahari Reserve and its three main fenced areas (adapted from Tokura et al., 2018). The unshaded area is the lion-exclusion area.

2.2 Vegetation

Tswalu comprises of five different vegetation types, which include Koranna-Langeberg Mountain Bushveld containing shrubs and trees, Gordonia Duneveld with grasses, Gordonia Plains Shrubveld with dwarf shrubs, Olifantshoek Plains Thornveld with

woody short shrubs and Kathu Bushveld (Mucina and Rutherford 2006; Tokura et al., 2018). Dominating trees in the reserve include *Boscia albitrunca, Vachellia erioloba* and *Terminalia sericea* (Roxburgh, 2010). Shrubs include *Rhigozum sp.* and *Senegalia sp.,* and grasses include *Aristida sp., Anthephora sp., Eragrostis sp.,* and *Stipagrostis sp.* (Mucina and Rutherford 2006). My study site was in the Gordonia duneveld along the Koranna-Langerberg mountains, an area where bat-eared foxes commonly occur.

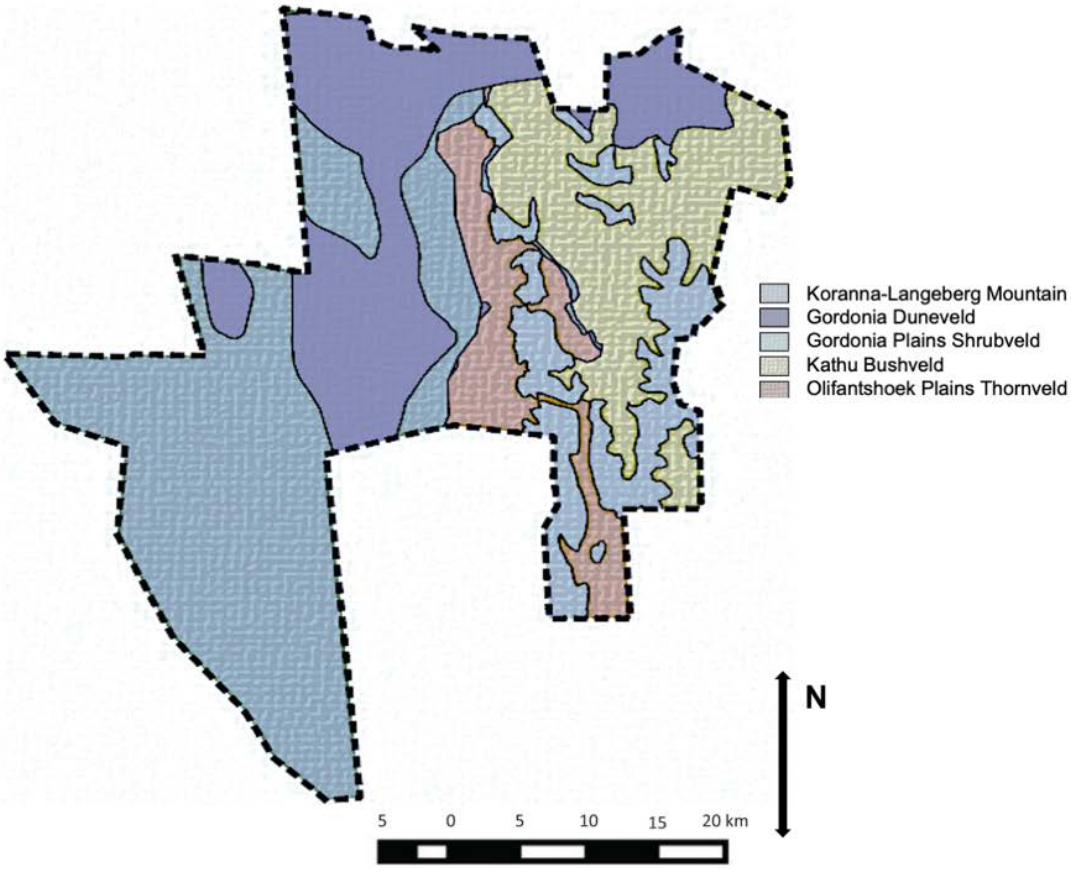


Figure 2.3: Tswalu Kalahari vegetation types (image adapted from Tokura et al., 2018).

2.3 Weather

Tswalu rainfall occurs during the hot months of the year, usually from November to April. To determine rainfall over my one-year study from March 2019 to March 2020, and beforehand (to examine delayed effects of rainfall), I acquired monthly rainfall measures from four rainfall gauges (Kraal, Witberg, Gosa and Namakwari) placed in and near the area in which I was working (Figure 2.4). Namakwari rainfall gauge is placed ~4.2 km away from Kukama (one of the study sites where I observed bat-eared foxes). I therefore used the Namakwari rainfall gauge to indicate rainfall that occurred in Kukama. I observed bat-eared foxes in three other locations, namely, Witberg, Kraal, and Gosa (Figure 2.4).

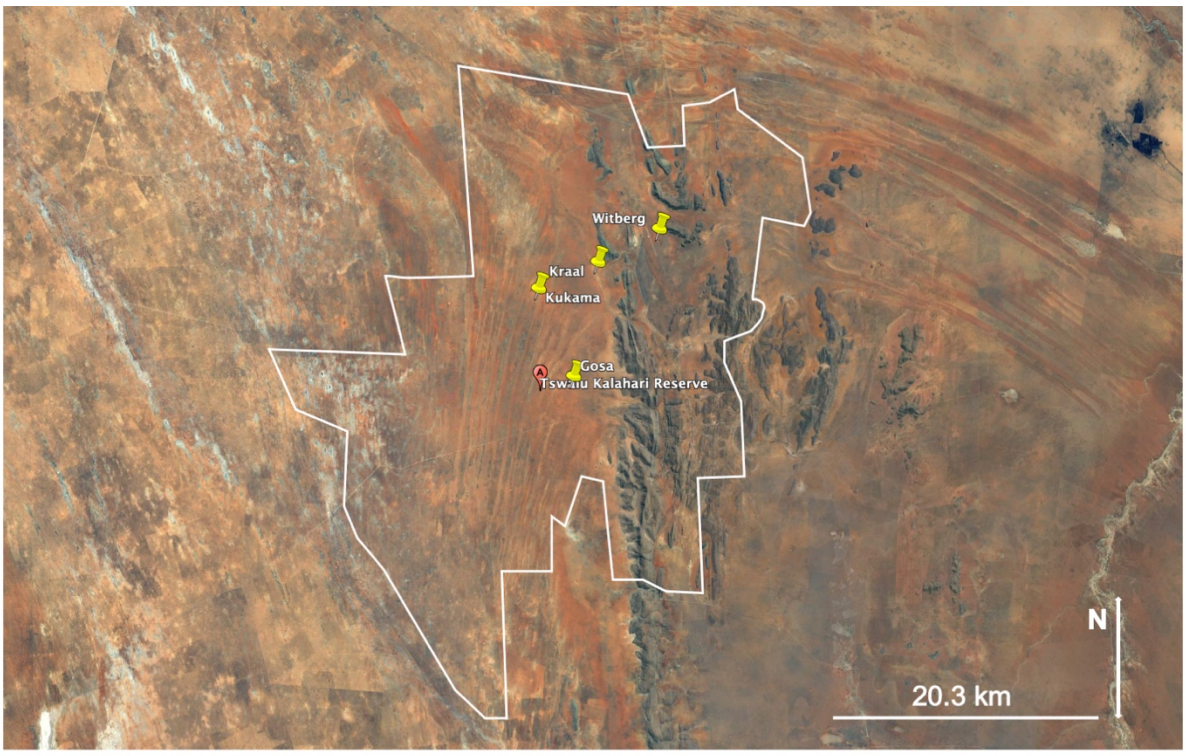


Figure 2.4: A map of Tswalu Kalahari Reserve showing bat-eared fox study locations and rainfall data collection sites (yellow pins, Google Earth, 2021).

To assess the heat load on bat-eared foxes, I measured black globe temperature using an iButton data logger (HOBO temperature/relative humidity data logger, Onset Computer Corporation, Massachusetts, USA). It had been shown previously that environmental temperatures showed similar readings across the bat-eared foxes' range (Weyer, 2018; W. Panaino, unpublished observations). I positioned the iButton

in the centre of a 150 mm copper globe painted matt black (Hetem et al., 2007) and placed ~17 km from where the foxes ranged. The black globe was not placed in the area where foxes ranged to avoid damage from free-living wildlife. I used black globe temperature as an index of heat load as it integrates the effects of air temperature, solar radiation, and wind speed. The black globe temperature provides a single index that describes the thermal environment of an animal (Hetem et al., 2007). The temperature data logger recorded temperatures at 30-minute intervals during the year of study (March 2019 to March 2020). I calculated the mean monthly temperature during the year of study and the daily means.

2.4 Ethics and permits

The University of the Witwatersrand Animal Research Ethics Committee (AREC) approved the procedures of the outlined research under clearance number 2019/04/21 CL and the Department of Environment and Nature Conservation, Northern Cape, provided a permit under the reference number OBD 1346/2019.

2.5 Invertebrate prey availability and grass cover

I measured invertebrate prey availability, consisting of ants (Hymenoptera), termites (Isoptera), spiders (Arachnids), scorpions (Scorpiones) and beetles (Coleoptera). I used 200 pitfall-traps, placed every second month over two days (100 pitfall traps per day) of each transect month of the study period. During the study period, I measured invertebrate prey using the same transects within a variety of vegetation types throughout the Gosa study site. I used the same transects sites that were previously used by our team members (Weyer, 2018). The invertebrates were collected to determine if there was an association between the invertebrate prey availability in pitfall traps with the invertebrates found in bat-eared fox scats (section 2.6 below). I used a 50 m tape measure to mark the transect length of 50 m (Figure 2.5). The 200 pitfall traps (50 ml conical sterile centrifuge tubes, Accumax, Gandhinagar, India) were placed along the transect at the same transect site (Gosa) every second month. I used a total of 20 transects, in which each transect consisted of 10 pitfall traps (200 pitfall traps in total), placed 5 m apart over the 50 m distance. I placed the pitfall traps in the

ground, with the opening of the trap level with the ground surface as shown in Figure 2.6. A solution of antifreeze and water was mixed in a 5 L bottle and contained 100 ml of antifreeze per 1 L of water. The solution aided in trapping invertebrates and prevented evaporation of the solution, which then allows trapped invertebrates to remain within the trap. Each trap contained 20 ml solution of antifreeze (SF radicool, Castrol, Johannesburg, South Africa) and water (Figure 2.7).



Figure 2.5: Using the 50 m tape measure to lay out the transect (Photo credit: Wendy Panaino).

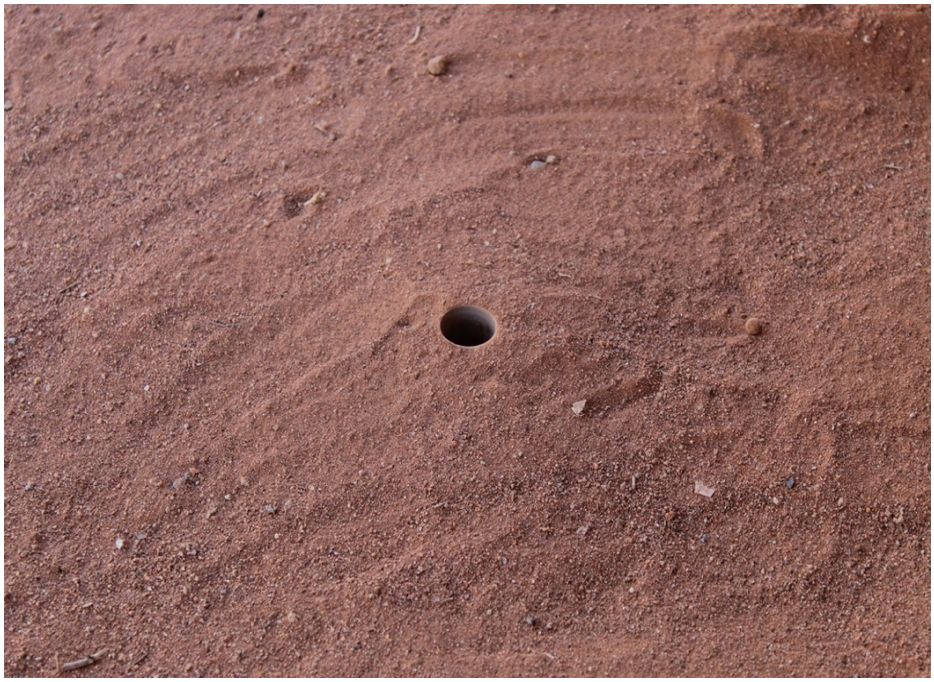


Figure 2.6: Pitfall trap in the ground (Photo credit: Valery Phakoago).

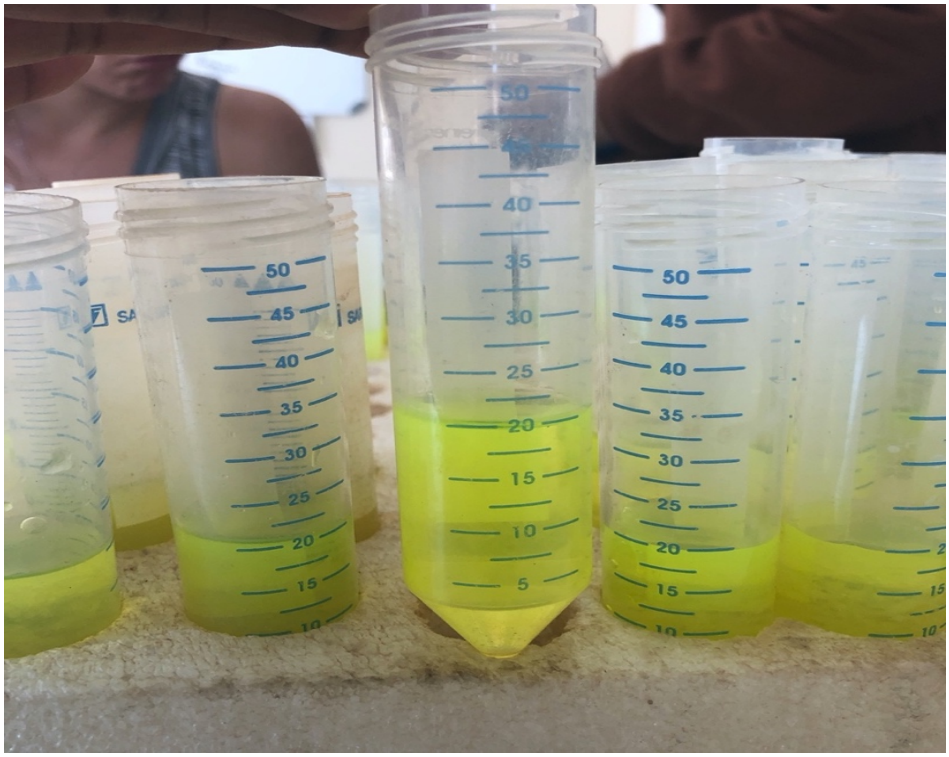


Figure 2.7: Centrifuge tubes with 20 ml of antifreeze solution (Photo credit: Letsema Molete).

Every two months I set out the 20 transects placed in two consecutive days, with the traps open for four days at a time. On the day of collecting the traps, I removed live invertebrates such as (Scorpiones) immediately to avoid any harmful stings. I counted the removed large live invertebrates and noted the number. I then collected the older trapped invertebrates for analysis. At each transect, I combined the content of invertebrates found in all ten traps into a 500 ml plastic bottle, containing 125 ml of water. In total, every two months, I collected 20 bottles of invertebrate insect prey to assess.

I used and adapted methods and guidelines from Weyer (2018) and W. Panaino (unpublished observations) to measure average grass cover. I used and measured grass cover using the same invertebrate prey transect. Grass cover was assessed to determine the availability of vegetation productivity, specifically grass. At exactly every 10 metres along the transect, I conducted a basic vegetation survey using a 4 m^2 (2 m x 2 m) plot, assessing the average grass cover percentage. To measure the monthly average grass cover percentage in each transect I counted the grass clumps within the 4 m^2 plot at every 10 meters (5 plots) that were covering the ground. For example, “transect 1” would have 5 plots of grass clumps per month of transect (Weyer, 2018). I then added the grass cover clumps from each plot to generate the grass cover of a transect. Thereafter, I added the grass cover from each transect to generate grass cover of transect month (for example April would have 20 grass covers from each transect). I then added the grass cover from each month of transect to generate the overall grass cover of the year of study (from April 2019 to March 2020). Thereafter, I generated the monthly average grass cover percentage by dividing the average grass cover from each transect month (seven months of transects) by the overall year grass cover and multiplied by 100.

I assessed the invertebrate prey availability from collected pitfall traps by first pouring the contents of the bottle through a 0.5 mm sieve (7 cm diameter stainless steel, Prestige, Johannesburg, South Africa) to remove any sand and plant particles, allowing only invertebrate prey to remain. To ensure that all invertebrates were counted, I manually removed the invertebrate prey items that were attached to plant matter using forceps (bioQuip forceps, bioQuip, Rancho Dominguez, USA). I then placed the prey items in a clear plastic container that had water only. Then with the

use of a bioQuip forcep, I then counted and separated each invertebrate species. Thereafter I weighed the invertebrates per species and placed the species into a microcentrifuge tube (15 ml sterile microcentrifuge tube, Accumax, Gandhinagar, India) with pure alcohol solution, labelled with the transect name, the invertebrate species, the weight, date assessed, and the number of invertebrates counted. In each transect, I calculated the number of invertebrates found per trap. To calculate the number of invertebrates found per trap, I added the number of each invertebrate species from each month and divided the value by the number of pitfall traps retrieved from transects. To identify each species found in the pitfall traps, I used Weyer (2018) invertebrate photo reference to identify ants and termites. I then used an invertebrate species reference collection of previous species found in pitfall traps (compiled by the Kalahari Ecosystem Endangered Project).

2.6 Bat-eared fox diet

I opportunistically collected scat samples from bat-eared foxes during each month of the study period from study sites where I observed bat-eared foxes. I collected bat-eared foxes' scats to assess diet and to quantify the composition of the diet. I collected fresh scats when I had an encounter with bat-eared foxes, and when there was an observation of defaecation. Once the foxes had defaecated and moved away, I collected the scat. Bat-eared fox scats have a thick cylinder shape that is 5 cm to 8 cm long, as shown in Figure 2.8. I distinguished their scats from those of other small carnivores, Cape foxes (*Vulpes chama)* and black-backed jackal (*Lupulella mesomelas)*, by shape and size. I stored the scat samples in a sealed Ziploc plastic bags (200mm x 250mm Ziploc bag, Glad, Johannesburg, South Africa), placing them in a freezer at -18°C until a later date for analyses.



Figure 2.8: Bat-eared fox scat droppings. (Photo credit: Letsema Molete)

I opportunistically collected dry (older) scats by walking in an area where I had previously encountered bat-eared foxes or where other Tswalu researchers had reported bat-eared foxes, as well as near dens. I categorized the dry scats based on their colouration; a more greyish colour would indicate scats that were at least a week old and black/brown would indicate one- or two-day-old scats. I only collected the one- or two-day-old scats as dry scats. I collected dry scats that had dried by natural sunlight in the field, then stored these scats in sealed Ziploc plastic bags in a room at a temperature of approximately 20°C. For the period of the study, I collected a total of 82 distinct scats.

I initially tested the use of natural sunlight to dry the fresh scats, and I found that baboons came to the areas where the fresh scats were placed. To avoid disturbance of the content in the scats, I reverted to freezing the scats. To determine what the bat-eared foxes had eaten, I took each fresh scat sample out of the freezer, placed it in a container in the oven at 70°C to thaw for 30 minutes and to remove ice along with liquid water. I weighed the scats using a scale (Professional digital scale 500 g/0.05

g, Lasa, Johannesburg, South Africa). Thereafter I soaked each scat in warm water for 30 minutes and washed it through a sieve with 0.5mm mesh holes for organic (prey mandibles, prey head, body capsules, grass, and seeds) and inorganic components (sand) to be separated. The sieve allowed sand to easily pass through the holes, while leaving prey items to remain on the sieve. I then dried prey items that remained after sieving in an oven at 70°C for ~24 hours and weighed the scats again. As the dry scats were not frozen, there was no need to thaw the scats. I analysed the dry scat samples using the same method as for the fresh scat samples after thawing.

I assessed the monthly diet from scats by calculating the number of invertebrates per scat. Due to the large amount of prey items that were found in the scats, each scat was sub-sampled into 0.5 g x 5 sub-samples (Figure 2.9) of the washed and dried scats to help identify and quantify the scats. In each scat, I counted each prey item individually and quantified it to its mass contribution per scat. The invertebrates per gram of scat was calculated by counting the number of each prey species in a scat, divided by the weight of the overall sub-sample (~2.5 g) of the scat. The same calculation was used when calculating the mass contribution of individual/invertebrate per scat for the category of “other”. I analysed each sample by using a stereo microscope (Olympus SZ 27368, Olympus, Tokyo, Japan) to identify species.



Figure 2.9: Sub-sample size of washed and dried bat-eared fox scats containing invertebrate prey consumed (Photo credit: Letsema Molete)

For the microscopic scat analysis, I used six categories to help identify and group each prey species. These were ants (Hymenoptera), termites (Isoptera), beetles (Coleoptera), scorpions (Buthidae), spiders (Arachnids) and “other” (plants, seed, fur or hair, invertebrate body capsules) as shown in Figure 2.10.

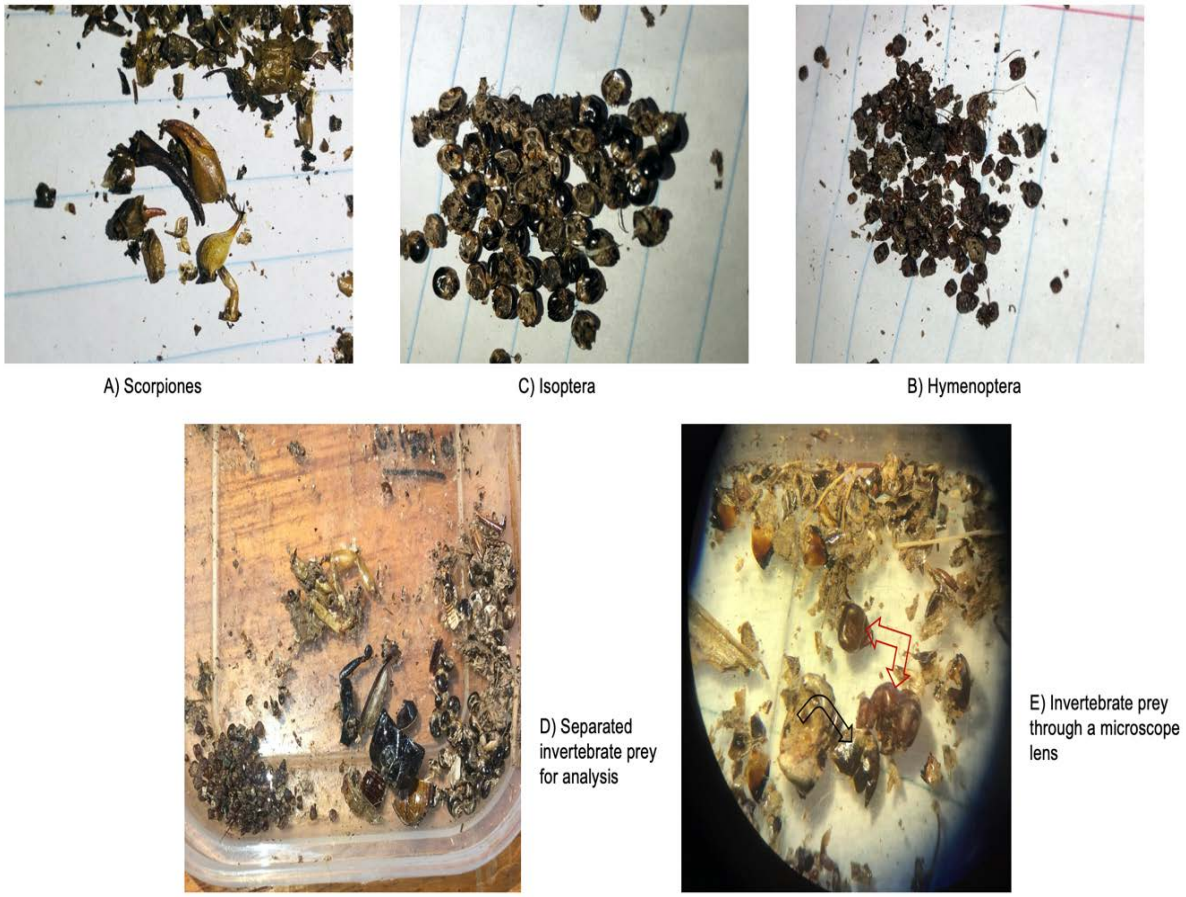


Figure 2.10 A to E: Shows invertebrate prey species during analysis. Picture "A" shows Scorpiones body parts, "B" shows Isoptera head capsules, "C" shows Hymenoptera head capsules. In picture "D" it shows invertebrate prey species separated for analysis and "E" shows invertebrate prey items (red arrows showing ants head capsules and black arrow showing termite head capsules) found in the scats of bat-eared foxes, through a microscope lens (Photo credit: Letsema Molete).

To help identify prey items, I used photo references from Weyer (2018) for ants and termites, Lemming (2019) for scorpions and Picker et al. (2019) for beetles. I identified termites to species level (two termite species). To help identify other species, I used the elytra, mandibles, abdomen, and head capsules to identify beetles and the cephalothorax and opisthosoma to identify scorpions. In some cases of body capsules or body cavities found in the scats were difficult to identify whether the capsules belonged to spiders, caterpillars, or grubs, therefore the body capsules were placed in the category of "other". To ensure that I did not overestimate the amount of prey

occurrence, two pincers would indicate one scorpion, one head capsule would indicate one prey item (ants, termites, beetles) and two elytra would indicate one beetle.

2.7 Activity periods of bat-eared foxes

I initially attempted to habituate groups or pairs of bat-eared foxes for a period of three months, from April 2019 until June 2019. To habituate the bat-eared foxes, I attempted to approach the animals both on foot and with the use of a vehicle. When on foot, I scattered raisins as an attractant while I walked slowly towards the bat-eared foxes, keeping to a distance of at least 30 m to 40 m away. When I used a vehicle, I approached a group or pair of bat-eared foxes while keeping a distance of approximately 30 m to 50 m, gradually approaching the foxes closer and stopping the vehicle whenever the foxes appeared to be disturbed by my presence. The foxes did not show any interest in the raisins during the period of the habituation, despite bat-eared foxes in another area previously having been habituated with the use of raisins (A. le Roux, personal communication). The habituation process was conducted to allow foxes to be acclimatised to human presence and for the planned process of capturing them to implant body temperature loggers. The foxes at Tswalu were skittish and ran away when I approached on foot. I was only able to approach the foxes while in a vehicle. I started recording times when I observed active bat-eared foxes from June 2019 until March 2020. I used binoculars to observe bat-eared foxes (Nikon Prostaff 7 10x42, Nikon, Melville, USA) and a spotlight (used at night). I remained at a distance of approximately 20 m to 30 m away from the bat-eared foxes. When I encountered a group of bat-eared foxes I focused on one individual to ensure accuracy of behavioural observations and collect the observation of the one bat-eared fox as a sample size.

To study the activity periods of bat-eared foxes, I recorded all observations of bat-eared foxes across the reserve to view the periods in which the bat-eared foxes were active. I observed bat-eared foxes in the four study sites shown in Figure 2.4, throughout different periods of the day I considered bat-eared foxes to be active when I encountered foxes walking or foraging and incorporated that activity as an observation. When bat-eared foxes were resting/sleeping, I considered the bat-eared

foxes inactive. Using the “speech voice over” in a cell phone to take notes, I noted the date and time I observed bat-eared foxes. When I encountered the bat-eared foxes, I recorded the time from that initial encounter to the time of final observation. When the foxes moved further into the distance or away because of my presence such that they could no longer be observed, I moved to a possible nearby road to try and locate the same group. When I could not locate them again after 15 to 30 minutes, I left the area. To avoid biased data in observing activity periods, team members conducting research at Tswalu assisted with collecting observations of bat-eared foxes when working around my study sites. I obtained a total of 149 days of observations and a total of 171 observations during the year of study. I then compiled the seasonal active times of bat-eared foxes across all four of my study sites using the time I observed the bat-eared foxes and the date I observed the bat-eared foxes.

2.8 Data analysis

I conducted analyses in Excel © 2020 Microsoft and R Studio (R version 4.0.3 (2020-10-10), Copyright © 2004-2020, The R Foundation for Statistical Computing and R studio, Version 1.3.1093, © 2009-2020 RStudio, PBC). In my analysis, I considered $P < 0.05$ as the critical level of statistical significance.

I calculated the average rainfall from four rain gauges across the reserve where scats and transects were collected. I used rainfall acquired from the Gosa study site as it was the area where transects were conducted. I then determined monthly rainfall from the study site Gosa and tested for Pearson’s correlation to test the relationships with average grass cover percentage and average black globe temperature over the year of the study. I also used Pearson’s correlation to test whether rainfall (from Gosa) during the three months of transects before the study period had a relationship with average grass cover percentage (allowing time for subsequent growth of grass). To do so, I calculated the average rainfall in the transect study site (Gosa) during the three months of transects before the study period (Sept 2018 to March 2020) and tested that average rainfall with the average grass cover percentage in the transect site (Gosa) during the year of study (March 2019 to March 2019). I used Pearson’s correlation to test the relationship between average grass cover percentage and prey

availability from pitfall traps and the relationship between prey availability and average rainfall during the months of transects. I further assessed variation of seasonal diet in bat-eared foxes using scats (invertebrates per gram found in scats). I then tested the relationship between invertebrate prey per pitfall trap and invertebrate prey per gram found in the diet (scats) using Pearson's correlation. I then described the seasonal active period of bat-eared foxes using observations obtained.

In addition to using correlations on data averaged across transects per month, I performed robust linear mixed models with raw rainfall data as the fixed effect, and raw transect data and month as random effects. Outcome variables were percent grass cover, and the average number of ants, termites, beetles, spiders, and scorpions per trap. All models yielded confidence intervals that included zero (no effect), and therefore we choose to report the simplest model, which was the correlation analysis.

CHAPTER 3

RESULTS

3.1 Weather

3.1.1 Rainfall

The mean annual rainfall from the four rain gauges positioned at my study site during the previous year, prior to my study period (March 2018 to March 2019) was 222 mm. During my study period March 2019 to March 2020, the annual rainfall, averaged across the four sites had a mean 200 mm ± 27 mm SD. Rainfall measured by the four rain gauges across my study area is shown in Figure 3.1. Overall rainfall that occurred during spring and summer of 2018 was lower compared to rainfall that occurred during spring and summer of 2019. Rainfall occurred mainly between November and April (April 2020 not shown as it was not part of my study period) and showed similar patterns in 2019 and 2020, except in February 2020, a month that was characterised by high rainfall, particularly at one site.

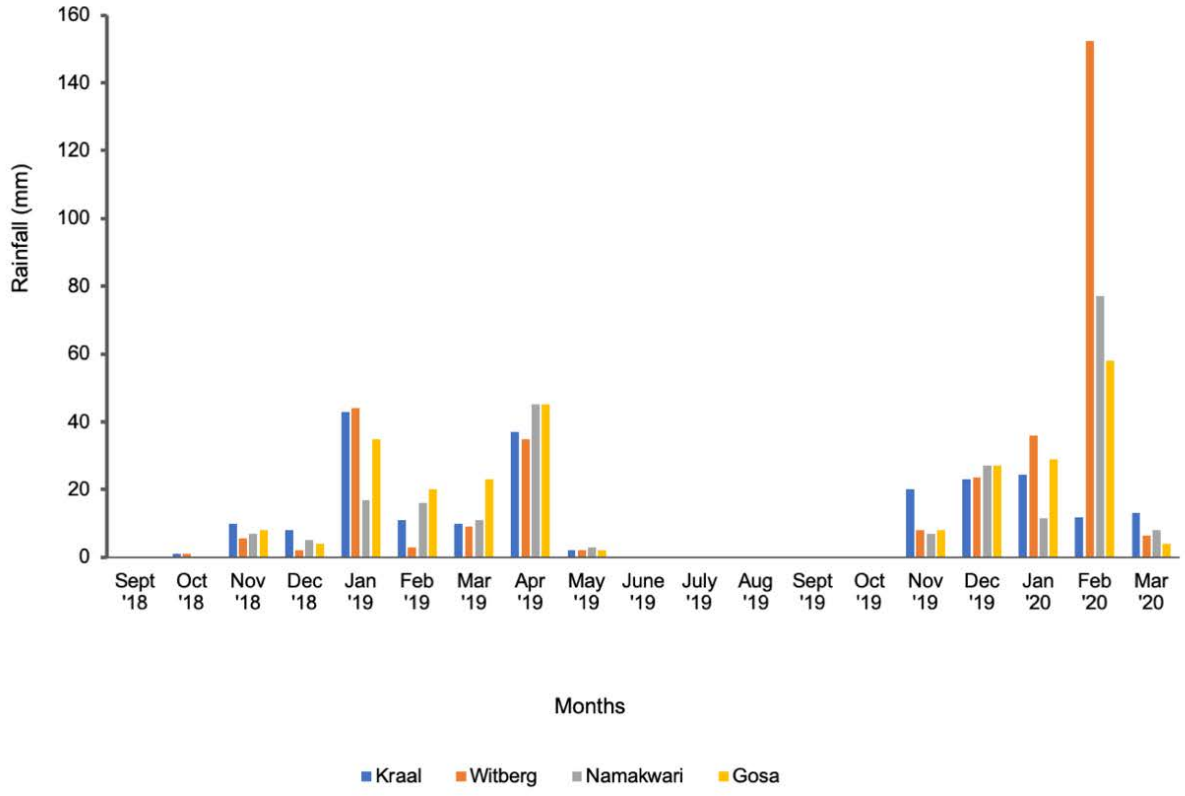


Figure 3.1: Rainfall occurrence during the year of my study, March 2019 to March 2020, including six months before the year of study, from four rain gauges (Kraal, Witberg, Namakwari and Gosa) across the study site.

Figure 3.2 shows the mean monthly 24-h black globe temperature during the year of study. The lowest mean monthly temperature recording during the year of study was 15°C in the winter months of June and July, while the highest mean temperature recording of 32°C was during the early summer. Further detail of the temperature variation in the extreme months of winter and summer are shown below.

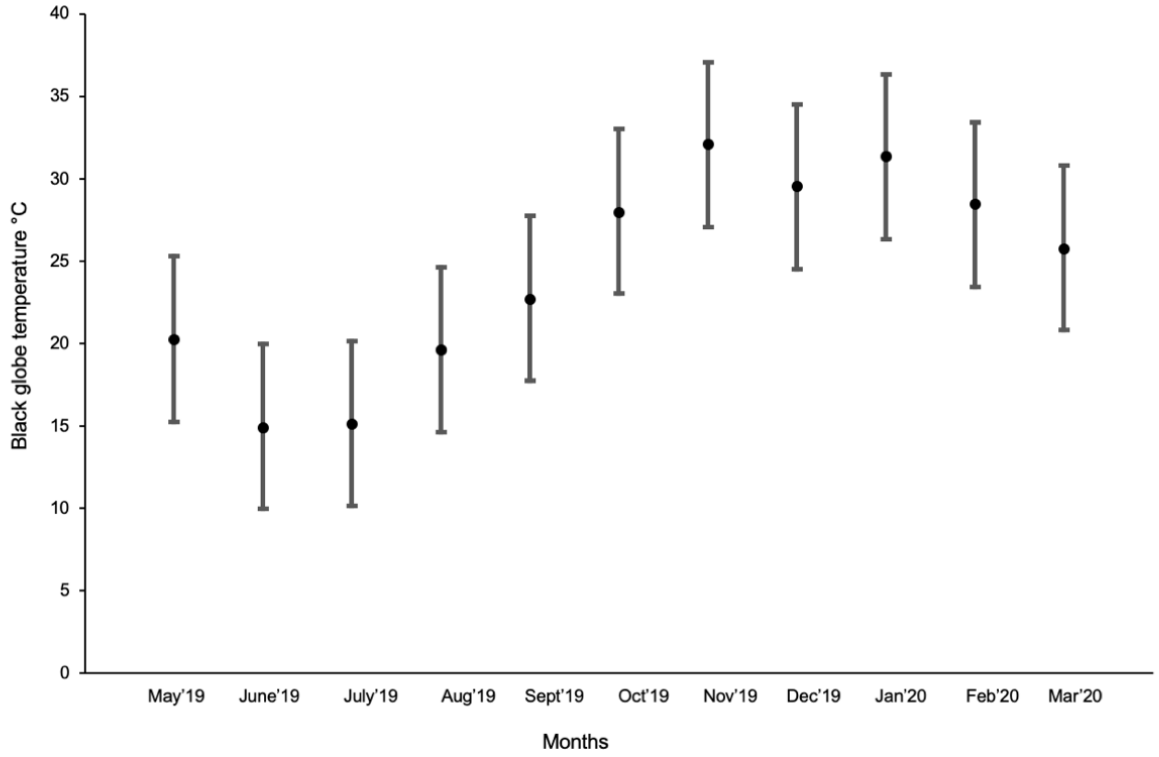


Figure 3.2: Mean ± SD of monthly black globe temperature during the year of study, from March 2019 to March 2020 (daily measurements were obtained only from late April, so monthly means are shown from May 2019 only). Temperature standard deviation showed minor variation during the year of study.

Black globe temperatures could range from below 0°C to more than 40°C (Figure 3.3) in winter. During the period of winter (June to August), average daily 24-h black globe temperature was 17°C (Figure 3.4), with maximum globe temperature occurring each day between 11:00 and 13:00 (Figure 3.3).

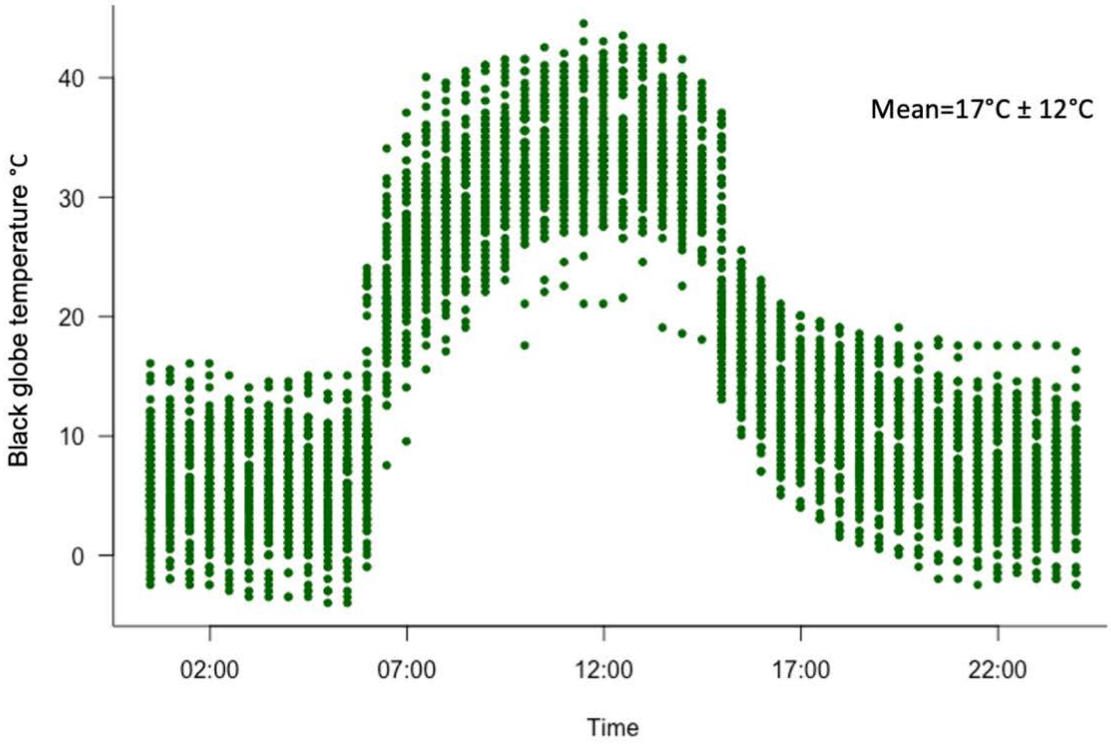


Figure 3.3: Temperature changes across a 24h cycle in winter, as measured by a black globe thermometer every 30 min during the winter of 2019. Data derived from measurements between June 2019 to August 2019.

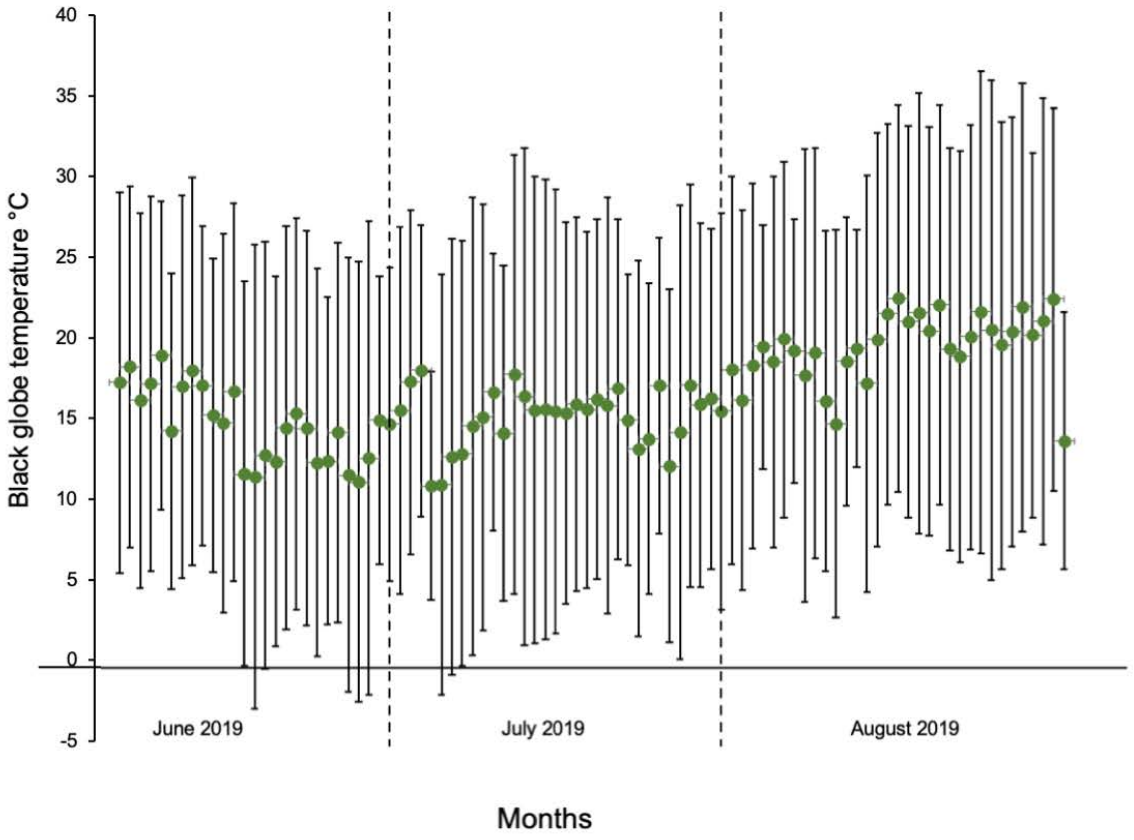


Figure 3.4: Back globe temperature showing daily mean ± SD of during winter of 2019

In contrast, in summer (December to February) black globe temperatures ranged between about 10 and 55 °C (Figure 3.5). Black globe temperatures (December to February) averaged 30°C (Figure 3.6) during summer, with maximum daily globe temperatures remaining high between noon and 17:00 (Figure 3.6). In both winter (Figure 3.3) and summer (Figure 3.5) globe temperatures were lowest just before dawn (between 23:00pm to 5:00am.

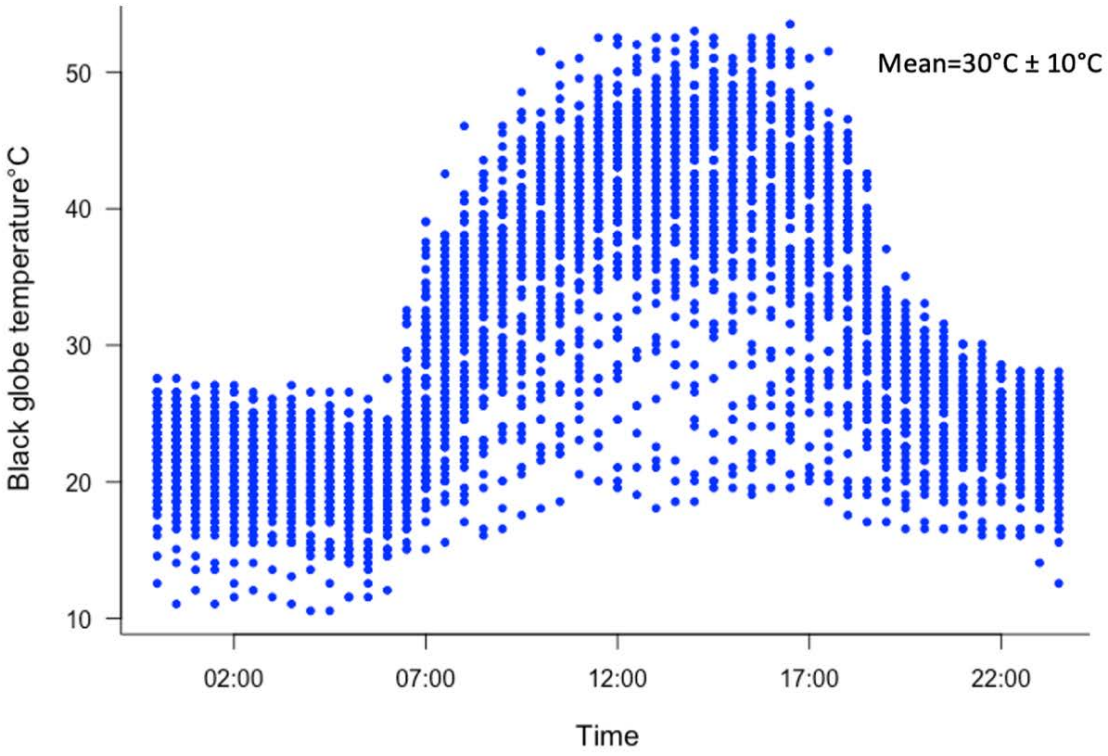


Figure 3.5: Temperature changes across a 24h cycle in summer, as measured by a black globe thermometer every 30 min during the summer of 2019 into 2020. Data derived from measurements between December 2019 to February 2020.

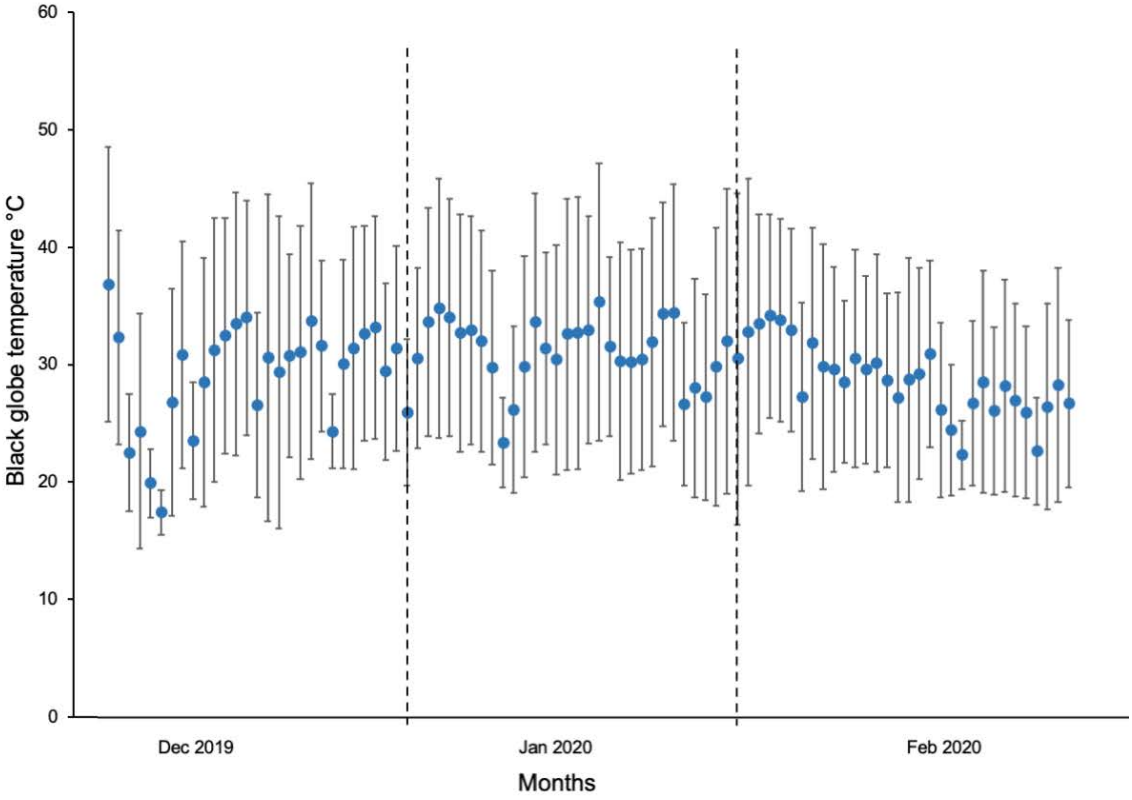


Figure 3.6: Daily mean ± SD of black globe temperature during summer of 2019 to 2020

3.2 Vegetation productivity (average grass cover percentage)

Figure 3.7 shows that average grass cover percentage was particularly low during the transect month of Sept 2018 (six months before the start of my study) but increased from that low by early summer (November 2018) before the start of my study in March 2019. During my study year grass cover percentage was at its highest in July 2019, as expected following summer rainfall that extended into May 2019 (Figure 3.1). The average grass cover percentage decreased from that peak into the following summer.

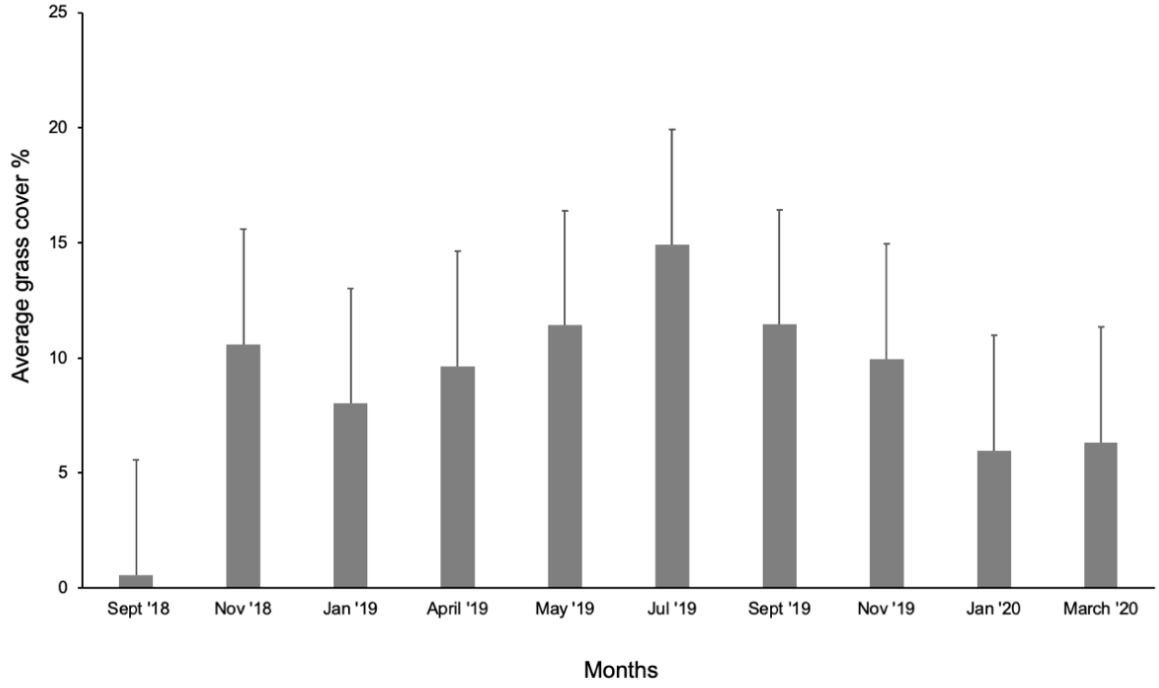


Figure 3.7: Grass cover percentage (mean + SD) during the months in which transects were carried out in the year of study (March 2019 to March 2020), including within the period three months of transects prior to the study year. Standard deviation for grass cover during the year of study showed slight variation.

3.3 Prey availability

During the months of transects I recorded invertebrate prey items caught in pitfall traps. I found that the overall average invertebrate prey items per trap during the year of study were13.28 Hymenoptera per trap, 0.68 Arachnida per trap, 0.38 Isoptera per trap, 0.13 Coleoptera per trap and 0.11 Scorpiones per trap. The overall average of Hymenoptera and Isoptera per trap during the three months of transects prior to the year of study was 27.00 for Hymenoptera per trap and 0.25 per trap for Isoptera.

Figure 3.8 shows invertebrate prey items per trap with the mean ± SD from pitfall traps (excluding Hymenoptera, as this order had much higher values per trap compared to all invertebrates, and so is shown separately) during the year of study and three months of transects prior to the year of study. Only Isoptera were found in traps in distinguishable numbers in all the transect months and were highest in number in July 2019.

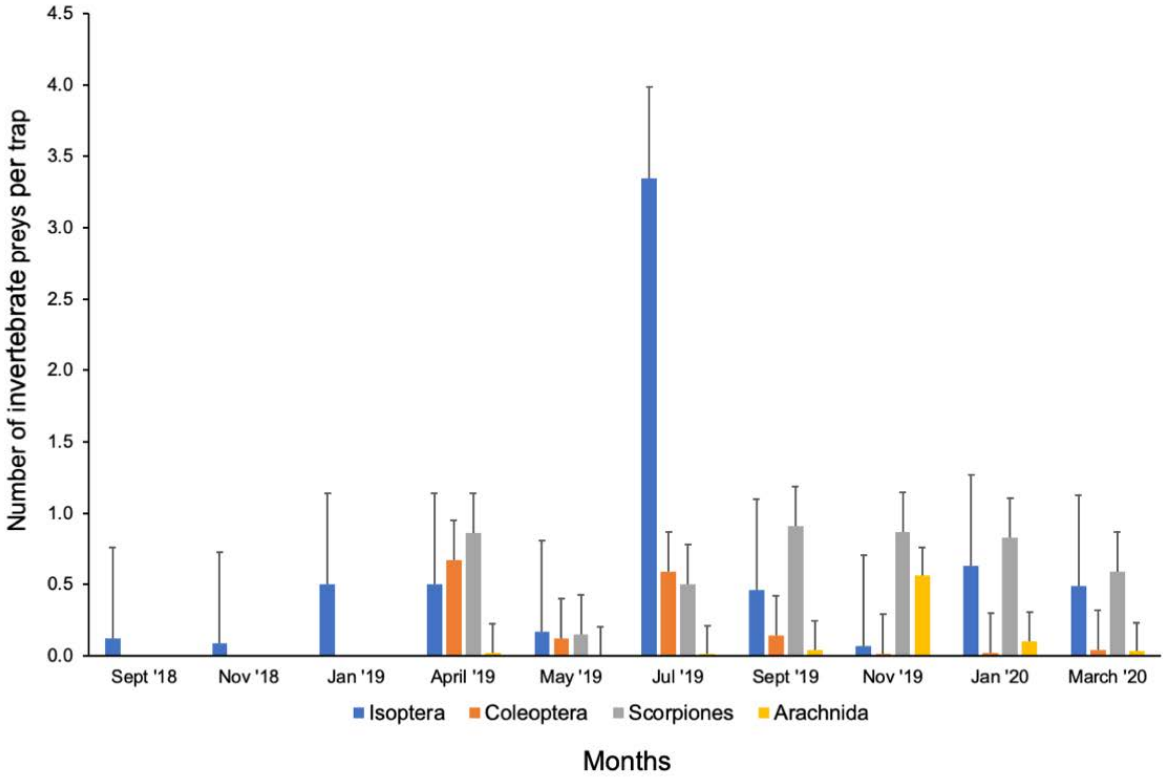


Figure 3.8: Prey availability per trap (mean + SD); Isoptera (blue), Coleoptera (orange), Scorpiones (grey), and Arachnida (yellow), during months of transects (April 2019 to March 2020) and three months of transects prior to the year of study (Sept 2018, Nov 2018, and Jan 2019). Hymenoptera per trap had much higher values compared to the shown invertebrate prey in the graph, and therefore shown in Figure 3.9.

The dominant item found in the traps was ants (Hymenoptera), as shown in Figure 3.9 for the year of the study and three months of transects before the year of study. Hymenoptera were highest in November 2018 before the start of my study and decreased to about half that value during the period of my study.

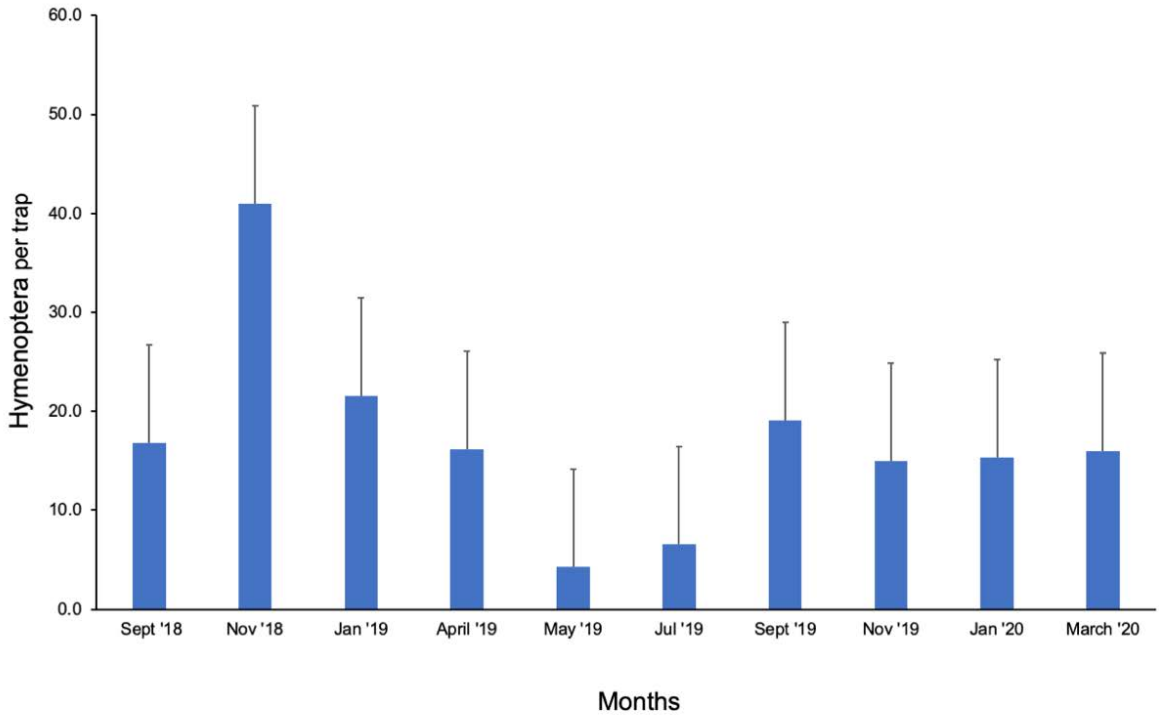


Figure 3.9: Hymenoptera per trap (mean + SD) during the year of study (April 2019 to March 2020), including months of transects prior to the year of study (Sept 2018, Nov 2018, and Jan 2019). Hymenoptera prey per trap showed that standard deviations did not vary during transects months of the year of study.

3.4 Relationships between environmental conditions, prey availability and grass cover

3.4.1 Environmental conditions and grass cover

Figure 3.10 shows no relationship between rainfall and average grass cover percentage from Sept 2018 to March 2020 for the months I carried out transects. There was no significant linear relationship between rainfall and grass cover percentage over this period (Pearson's correlation, r= -0.118, p= 0.744). Restricting the analysis to the data obtained in the year of my study only (March 2019 to March 2020) did not reveal a linear relationship either (r= -0.433 and p= 0.332).

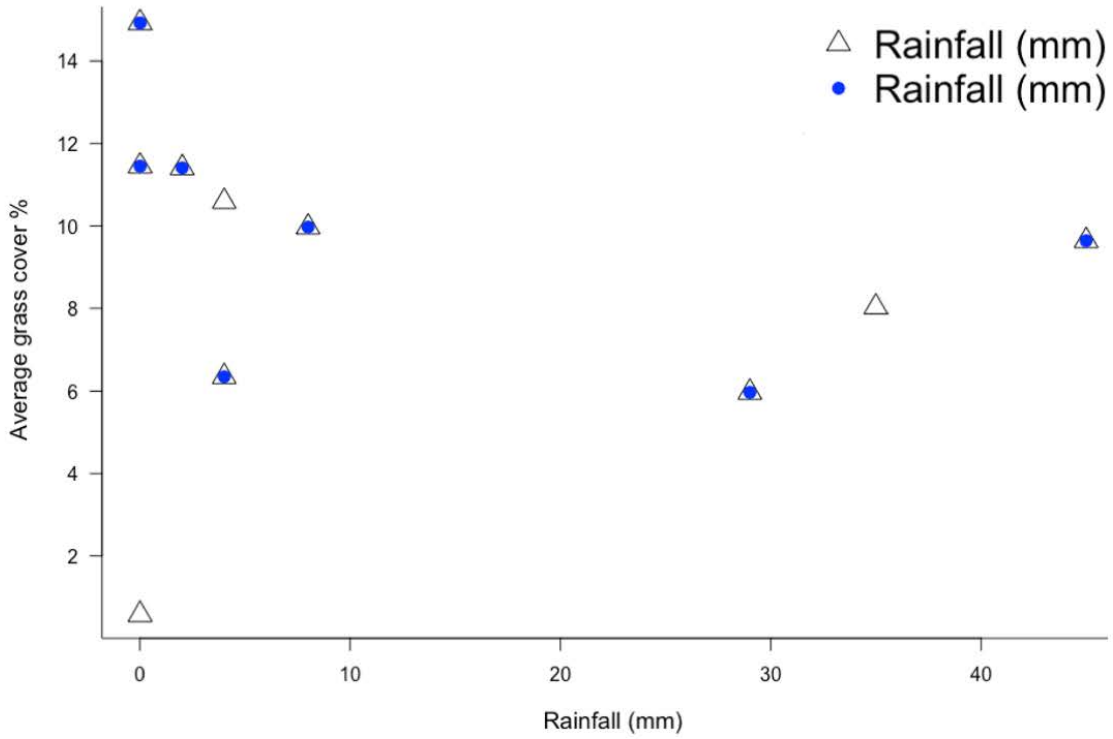


Figure 3.10: The relationship between rainfall and average grass cover percentage, with rainfall during three transect months prior to the year of study and months of transects during the year of study (from Sept 2018 to March 2020) shown by triangles, and the relationship between rainfall and average grass cover percentage obtained during the study year shown by blue circles (March 2019 to March 2020).

Grass cover percentage was also not linearly related to mean black globe temperature as shown in Figure 3.11 (r= -0.210 and p= 0.535) over the year of study, between March 2019 and March 2020.

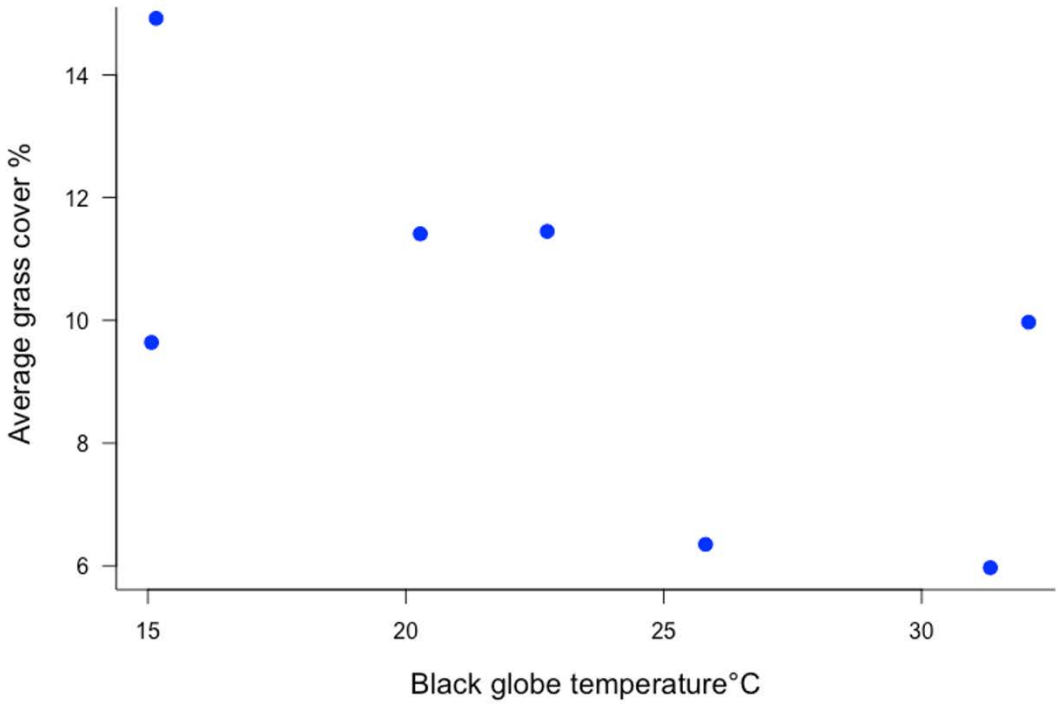


Figure 3.11: The relationship between average monthly 24-h black globe temperature and average grass cover percentage during transect months, over the year of study (March 2019 to March 2020).

3.4.2 Invertebrate prey availability and rainfall

I investigated whether rainfall influences prey availability by comparing monthly rainfall during transect months in the year of my study with the relative available invertebrate prey per trap found in pitfall traps during those months at the transect study site (Gosa). Figure 3.12 shows the relationship between rainfall at the transect study site (Gosa) and invertebrates per trap (Hymenoptera, Isoptera, Coleoptera, Scorpiones and Arachnida). Figure 3.12 shows that there were no significant linear relationships between rainfall and the various categories of invertebrate prey per trap during the year of study.

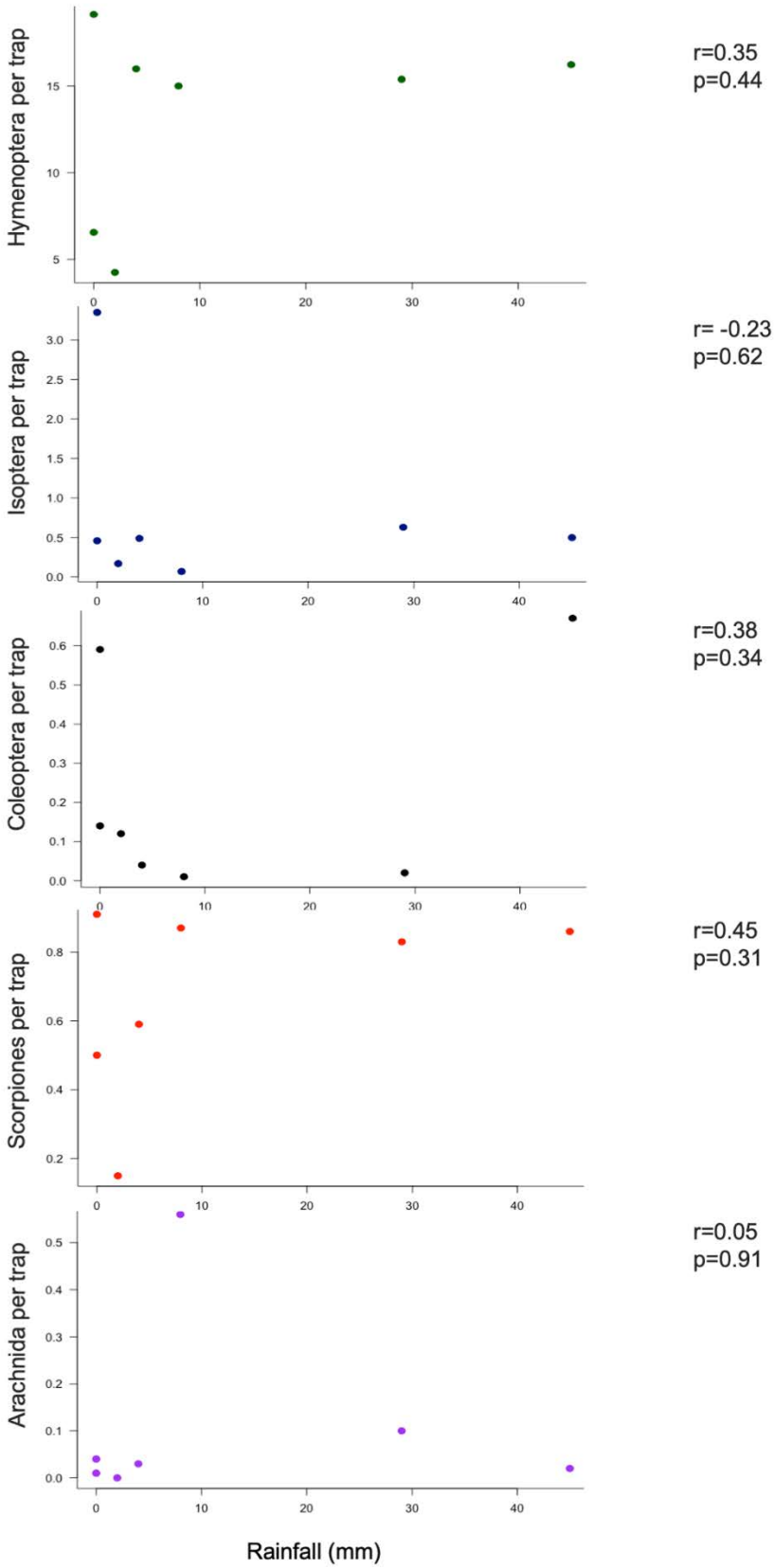


Figure 3.12: The relationship between rainfall and invertebrate prey per trap (shown in different colours to differentiate prey species) in transect months during the year of study (March 2019 – March 2020).

3.4.3 Invertebrate prey availability and average grass cover percentage.

I also compared average grass cover percentage during transect months in the year of my study with the available prey species found in pitfall traps during March 2019 to March 2020. Figure 3.13 shows the relationship between average grass cover percentage and Hymenoptera, Isoptera, Coleoptera, Scorpiones and Arachnida found in pitfall traps. Figure 3.13 shows that there were no significant linear relationships between the potential invertebrate prey availability found in pitfall traps and the average grass cover percentage.

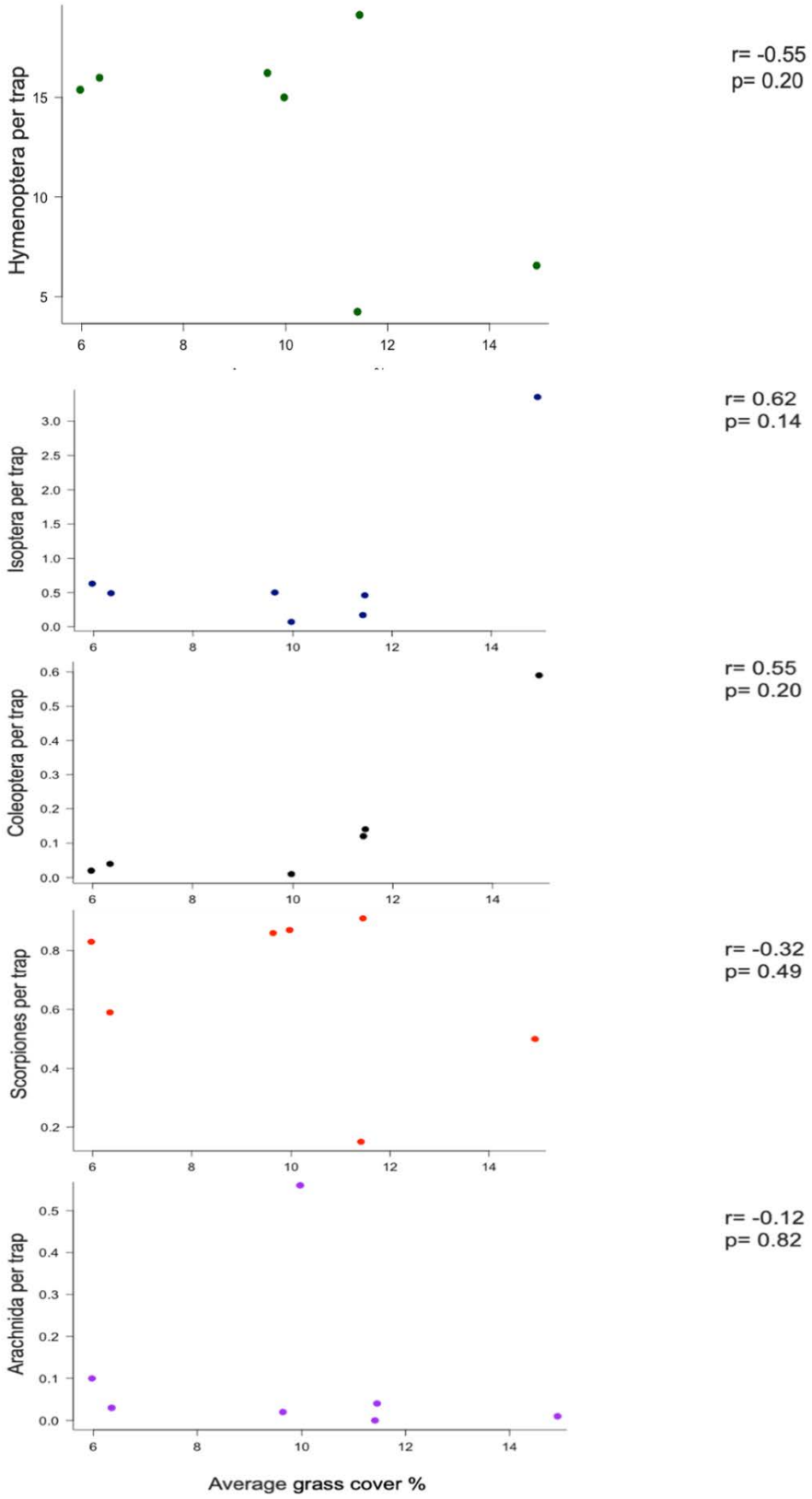


Figure 3.13: Average grass cover percentage and invertebrates per trap (in different colours to differentiate prey species) in transect months during the year of study (March 2019 to March 2020).

3.5 Seasonal diet of bat-eared foxes

3.5.1 Diet of bat-eared foxes based on scat analysis

Figure 3.14 shows the diet of bat-eared foxes based on scat analysis over the full period of the study, from March 2019 to March 2020. Overall, I found that termites (Isoptera) contributed more than half of the prey eaten, with 66 Isoptera per gram of scats during the year of study. *Hodotermes mossambicus* (Northern harvester termite) was the only termite species found in the scats of the bat-eared foxes. There were 21 ants (Hymenoptera) per gram of the scat and 4 beetles (Coleoptera) per gram of scat. Scorpions (Scorpiones) occurred as 1 item per gram of scat, while spiders (Arachnida) were not found in the scats of bat-eared foxes at Tswalu. The remainder of the diet included seeds, plants (grass and leaves), grasshoppers, worms (grubs) and animal fur ("Other").

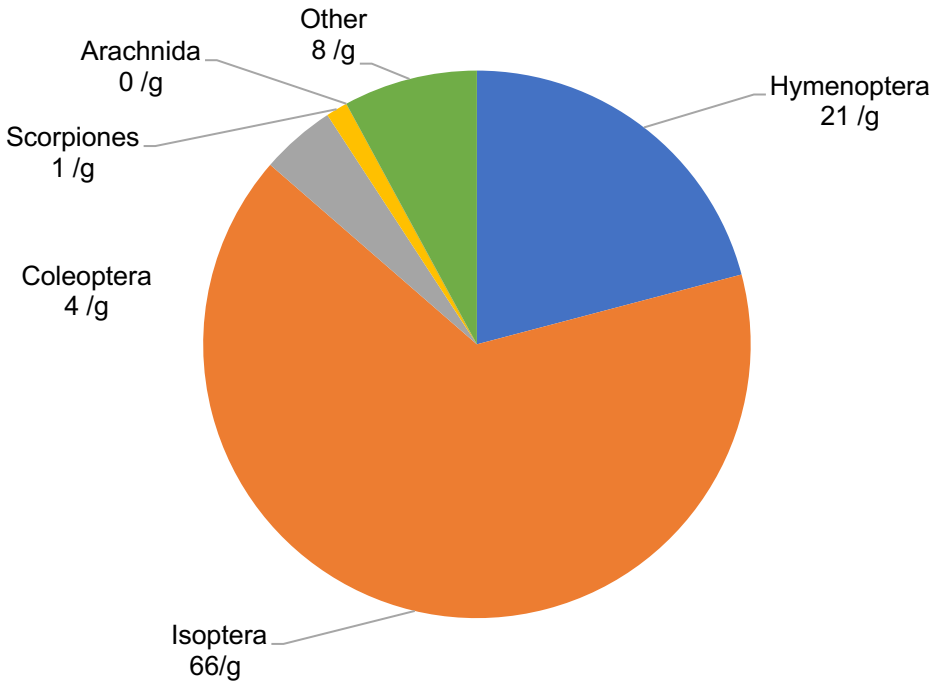


Figure 3.14: Categories of prey species per gram consumed by bat-eared foxes during the year of study (March 2019 to March 2020) as determined from scat analysis.

Figure 3.15 shows how the diet of bat-eared foxes varied seasonally over the study year. I collected 29 scats during autumn, 11 during winter, 26 during spring and 17 in

summer. I found that the most consumed prey, harvester termites (Isoptera), were the main prey consumed during autumn (March to May; 67 per gram of scat), winter (June to August; 64 per gram) and spring (September to November; 64 per gram). In summer (December to February), Isoptera contributed 48 items per gram to the diet of bat-eared foxes, while an increase of beetles (Coleoptera; ~14 per gram) was found compared to the other seasons. Termites, beetles, and ants (Hymenoptera) were consumed throughout the year, while there was relatively low intake of scorpions (Scorpiones), particularly during winter.

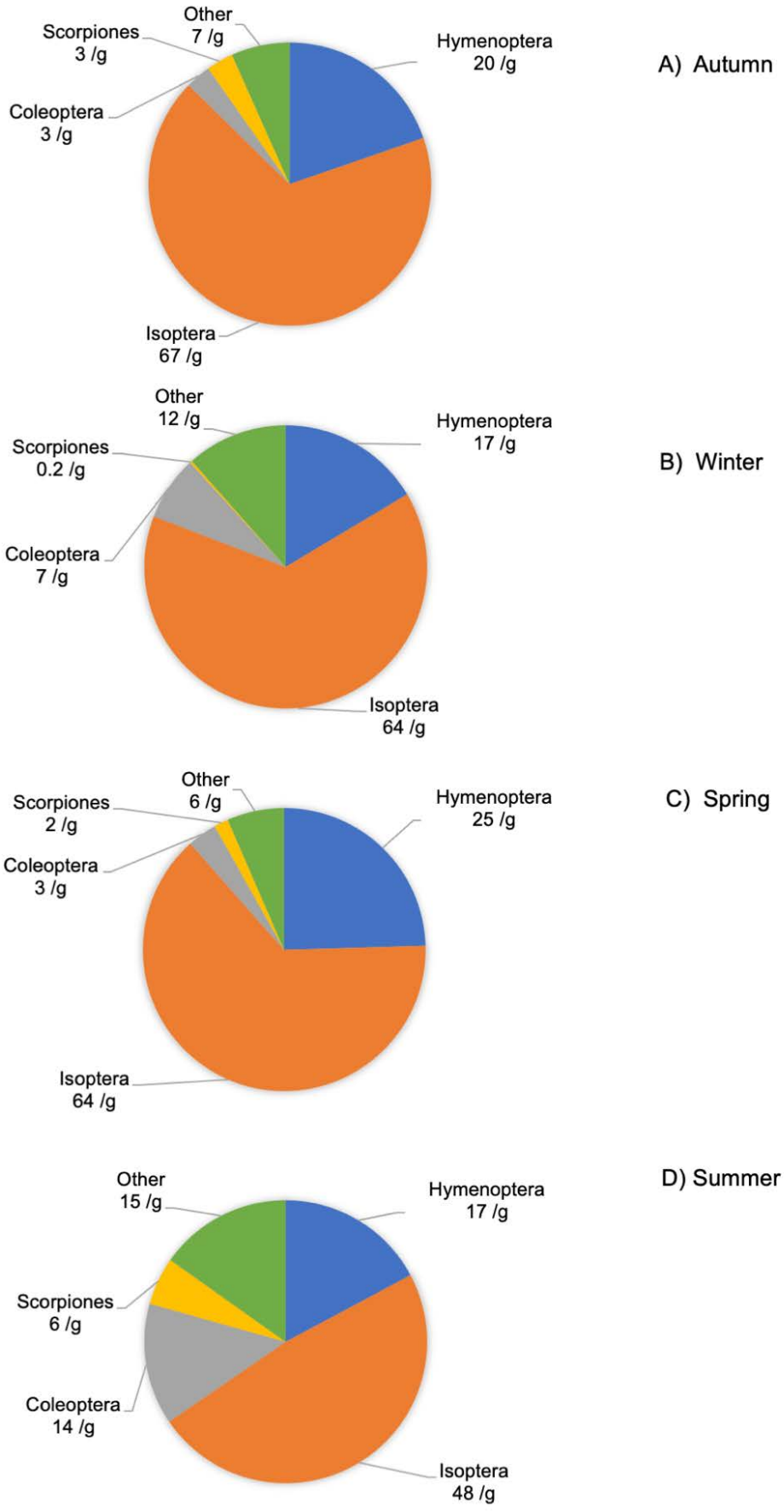


Figure 3.15: Categories of prey species consumed by bat-eared foxes each season.

3.5.2 Relationship between prey intake and prey availability.

I compared invertebrate prey per trap with the invertebrate prey species found in the scats of bat-eared foxes collected during transect months in the year of study. The prey items found in traps are expressed as numbers of individuals per trap while the prey items found in diet (scats) are expressed as invertebrates per gram of scats during transects months. Figure 3.16 shows the relationship between invertebrate per trap at the transect study site (Gosa) and invertebrate prey species in bat-eared fox diet. There were no significant linear relationships between the invertebrate prey from pitfall traps and the invertebrate prey from the bat-eared fox diet. For Coleoptera, there appeared to be a positive relationship between prey in the trap and in diet, with the correlation almost statistically significant (P=0.05).

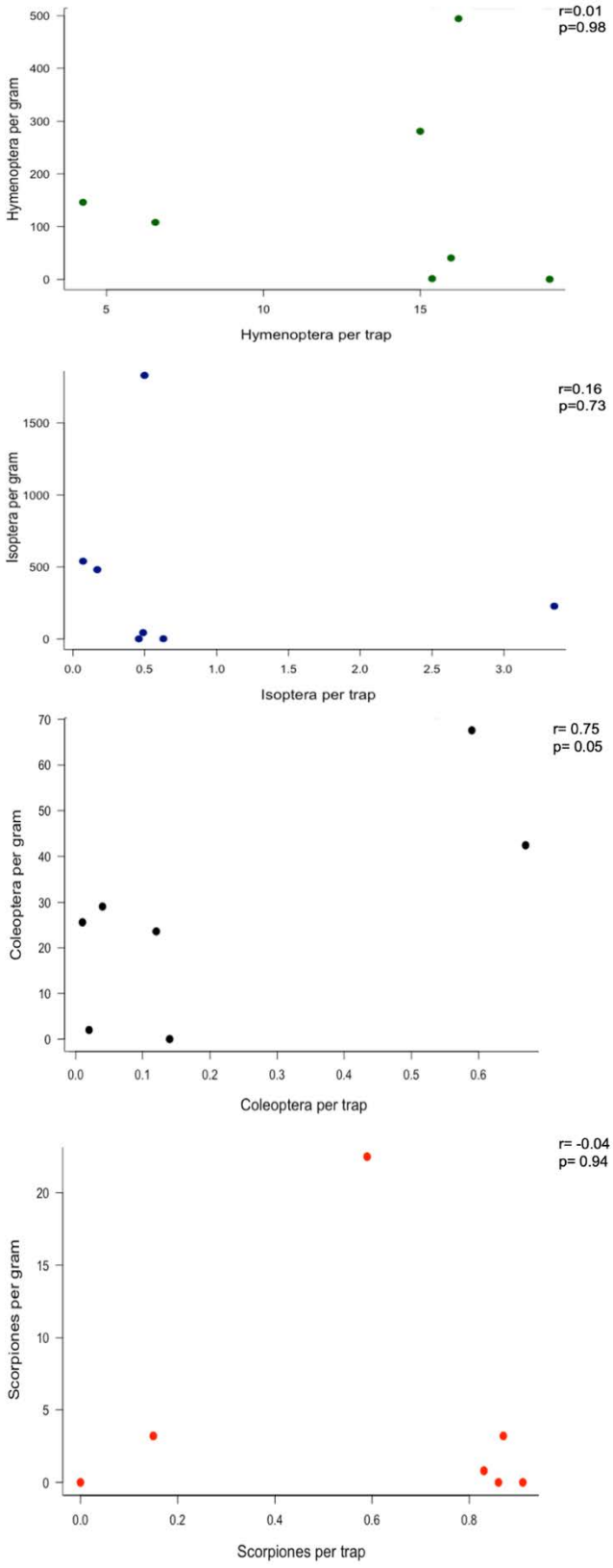


Figure 3.16: The relationship between invertebrate prey per trap and invertebrates in the scats (per gram of scat, indicated on the y-axis) of bat-eared foxes during the year of study (March 2019 – March 2020).

3.6 Behavioural activity

Figure 3.17 shows a seasonal overview of the bat-eared foxes' active periods. Bat-eared foxes exhibited more nocturnal activity compared to diurnal activity during the year of study. During the year of study, I had a total of 141 hours and 35 min of observations. In autumn, when I had 31 observations of bat-eared foxes, I found the foxes to be active between 18:00 and 21:00. In winter I had 17 observations of bat-eared foxes, with foxes active earlier in the day compared to in autumn. During spring I had 39 observations of bat-eared foxes, with the active periods similar to those in winter. In summer I had 99 observations of bat-eared foxes, with the foxes primarily active at night (nocturnal) except for a few occasions in the morning.

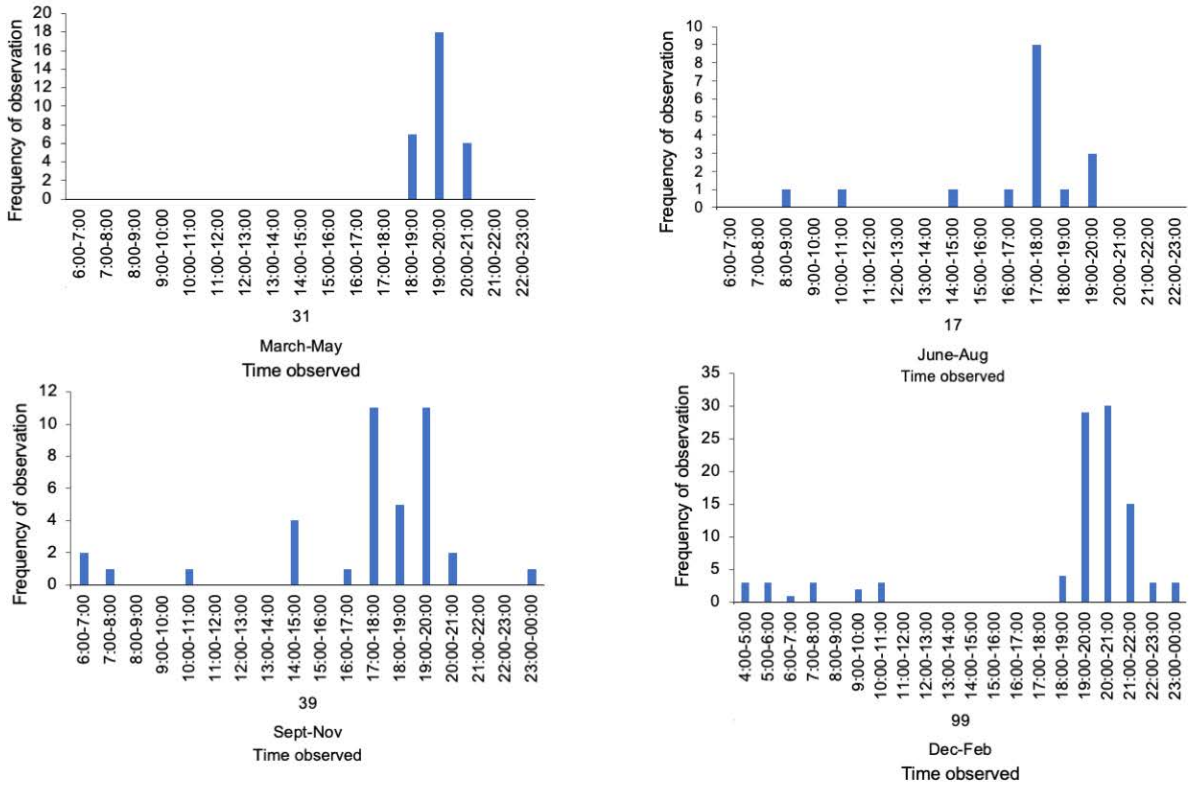


Figure 3.17: The active periods of bat-eared foxes during different seasons over the study year.

CHAPTER 4

DISCUSSION

I assessed the diet of bat-eared foxes over one year in the Kalahari by examining scats collected during that year. Like previous studies, I found that the most consumed prey of bat-eared foxes was Isoptera, *H. mossambicus*, with these termites making up about two-thirds of mass in the diet of bat-eared foxes over the year of study. Bat-eared foxes also consumed a relatively high proportion of Hymenoptera, with Hymenoptera making up ~21% of the diet by mass (Figure 3.14). Beetles and scorpions were also consumed, but at a much lower proportion (Coleoptera ~4% and Scorpiones ~1% of the diet by mass) during the year of study. Although spiders have been previously recorded in the diet of bat-eared foxes (Smithers, 1971; Stuart et al., 2003), I found that they were not present in the scats of bat-eared foxes during my study period, despite being found in pitfall traps in warmer months of the study year (Figure 3.8). I found that bat-eared foxes consumed other invertebrate prey which included grubs and grasshoppers, as well as seeds and other plant material. Plants present in the diet of bat-eared foxes consisted mainly of grass and leaves, indicating possible incidental feeding on these items when foraging on invertebrates. Few seeds and grasshoppers only occurred in scats collected during autumn and summer, while grubs were found in scats across all seasons.

Termites made up about two-thirds of the diet by mass in all seasons except during summer when they decreased to about half the dietary items (Figure 3.15). Previously it has been shown that bat-eared foxes feed mainly on two termite species, *H. mossambicus* and *Trinervitermes trinervoides* (Bothma et al., 1984; Klare et al., 2011). Although I found *T. trinervoides* in pitfall traps, only *H. mossambicus* were consumed by bat-eared foxes at my study site. When the proportion of termites in the diet declined in summer, bat-eared foxes increased the consumption of beetles (Figure 3.16). The consumption of beetles appeared to be associated with an increase in beetle availability at that time of year (Figure 3.8). Bat-eared foxes consumed ants throughout the year, with the proportion in the diet being slightly higher during spring and autumn compared to in winter and summer. Scorpions were consumed more during summer and autumn, when they were likely most active (during the hot and wet season) and more likely to be caught in traps, compared to other seasons (Figure 3.15).

Changing rainfall, as a direct effect of climate change, can influence food resources and the productivity of an ecosystem (Fuller et al., 2010; McNutt et al., 2019; Levy et

al., 2019). The occurrence of rainfall influences vegetation growth, and often some invertebrates will respond to the availability of vegetation (Whyte, 1985). Often invertebrate species will increase after rainfall that occurred in prior months (Dangerfield, 1998; Cumming and Bernard, 1997; Ridley and Raihani, 2007). I therefore assessed whether there was a direct relationship between rainfall and the numbers of invertebrate prey species found in pitfall traps during months of transects in the year of my study. My data revealed a low occurrence of rainfall and low invertebrate prey availability numbers, compared to previous years at the study site (Weyer, 2018; W. Panaino, unpublished observations). However, there was no significant correlation between rainfall and invertebrate prey per trap (Hymenoptera, Isoptera, Coleoptera, Scorpiones and Arachnida; Figure 3.12). One reason for the lack of correlation is likely to be months that had no rainfall during winter and spring. Another is that the generally low abundance of insects, except for ants, may not have translated into distinguishable differences in counts of insects in traps across the year. I also had a small sample size, with only seven transects during my study year. Further analysis of the data using robust linear mixed models also revealed no association between invertebrates in traps and rainfall. The invertebrate prey numbers therefore did not respond directly to the occurrence of recent rainfall in my study year. A response of invertebrates to rainfall may be associated with a response to food resources and the species' physiological survival during periods of no rainfall and low rainfall occurrence (Schowalter et al., 1999; Barnett and Facey, 2016). In addition to the possible short-term effects of rainfall, the intensity of previous droughts and prevailing environmental temperatures can further impact insect prey abundance (Braack, 1995). The year before I started my study was characterized by extremely hot and dry conditions, resulted in the area being classified as hyper-arid (see Figure 1, Fuller et al., 2021).

I nevertheless expected that average grass cover would respond to the occurrence of rainfall. Therefore, I tested whether there was a correlation between rainfall that occurred in the year of study and average grass cover percentage in corresponding months during the year of study. However, I found that there was no relationship between rainfall and average grass cover percentage (Figure 3.10). As the effects of rainfall on vegetation growth are likely delayed, I then investigated if there was a relationship between rainfall that occurred three months prior to each grass transect.

Again, I found that there was no relationship between previous rainfall and average grass cover during the year of study. The timing of rainfall events is considered essential in influencing the availability of food in an ecosystem (van Wilgen et al., 2016), and generally low occurrence of rainfall during the year of my study likely impacted the average grass cover percentage of the year of the study. Average grass cover percentage never exceeded 15% and varied seasonally, exhibiting an increase during the late autumn season and early winter season compared to spring and summer (Figure 3.7). The increase of average grass cover percentage during winter likely resulted from previous months of rainfall (Dudney et al., 2017), with rainfall occurrence in the preceding summer, and some rainfall extending into the month of May. High environmental temperatures that occurred in summer, during the main period of rainfall, may also have influenced grass growth, by decreasing water penetration into the soil and causing evaporation to occur at a rapid rate (van Wilgen et al., 2016; Dudney et al., 2017).

The abundance of many invertebrate species is dependent on the productivity of grass growth (Cumming and Bernard, 1997; Dudney et al., 2017). I therefore assessed whether the average grass cover percentage was correlated with the abundance of invertebrate prey, across the months of transects. In autumn and winter, when grass cover was highest, I expected invertebrate prey numbers in traps to increase. However, while Isoptera, Coleoptera and Scorpiones were caught in pitfall traps in autumn and winter, I found no linear relationships between average grass cover and the number of prey items in traps (Figure 3.13). Temperature may have been a confounding factor, as an increase of ambient temperature affects the metabolic rates of invertebrates, thermal tolerance, their distribution, and populations (Gillooly et al., 2001; Bale et al., 2002; Frazier et al., 2006; Musolin, 2007). *H. mossambicus* are known to increase their activity and be more available to predators during autumn and winter (Nel and Hewitt, 1969). I found that termites occurred in the traps with highest numbers in the winter of 2019, while ants were lowest in number in autumn and winter of 2019 (Figures 3.8 and 3.9). Herbivore invertebrate species are expected to increase above-ground activity during autumn and winter as a response to acquire food and avoid high temperatures, which are more common in summer (Nel and Hewitt, 1969). Some invertebrate species, however, are likely to increase above-ground activity during the evening in summer and make use of microclimates during the day to avoid

increased air temperatures (Conway, 2009). More detailed analyses of the activity patterns of the invertebrates preyed on by bat-eared foxes, together with abundance measures other than just pitfall traps, are needed to determine the seasonal variability of invertebrates and potential relationships with precipitation and grass growth.

Environmental temperatures also are likely to influence the relationship between vegetation and rainfall. As expected, globe temperatures varied seasonally over my study year, with lowest temperatures occurring during winter (June and July) and highest temperatures in summer (December to January). In summer, average black globe temperature was about 30°C, and despite the rainfall over this period, grass cover was low, only increasing from autumn. During winter average black globe temperatures were much lower (about 15°C) with no occurrence of rainfall, but higher grass cover compared to other seasons. I used black globe temperature as an index of heat load as air temperature does not reflect the influence of radiant heat in an environment. In arid environments like the Kalahari, the major factor affecting the heat load on organisms is solar radiation (Mitchell et al., 2018). High heat loads can be experienced on clear winter days, as shown by globe temperatures exceeding 40°C in winter (Figure 3.3). In winter, however, globe temperatures sometimes were below zero degrees Celsius, likely reflecting a large heat sink to the environment (Fuller et al., 2021).

There was very little nocturnal activity of bat-eared foxes in winter, as well as in autumn (Figure 3.17) possibly reflecting cold avoidance by the foxes. As indicated above, activity patterns of bat-eared foxes also may have changed in response to changing activity patterns of prey species, which also would be influenced by environmental temperatures. I did not assess 24h patterns on invertebrate activity but did assess how the availability of invertebrate prey in pitfall traps varied seasonally and influenced the diet of bat-eared foxes. I found that the overall diet of bat-eared foxes reflected the prey items found in the pitfall traps, with the exclusion of the termite *T. trinervoides* and Arachnida. Despite spiders being found in the pitfall traps from September 2019 to March 2020, there were no spiders in the scats (Figure 3.14). For prey items that were found in the scats, there was no relationship between the number of prey items found in traps and prey items in the scats except for Coleoptera, where a weak positive relationship appeared to be evident. Regardless of the availability of invertebrates, as

reflected by the pitfall traps, bat-eared foxes mainly consumed Isoptera and Hymenoptera. The number of termites in traps was highest in winter (Figure 3.8), but the number of termites in scats was similar in winter, autumn, and spring. The number of termites in the scats was substantially lower in summer, following very low numbers of termites in traps in November. Bat-eared foxes appeared to compensate for the reduction in termites in their diet in summer by increased feeding on beetles (Figure 3.15). Ants, the most abundant invertebrate in the traps in all seasons, were consumed throughout the year, making up about a fifth of the diet, in terms of items per scat, on average (Figure 3.14).

In agreement with previous studies (Kuntzsch and Nel, 1992; Klare et al., 2011), the most utilized dietary item for bat-eared foxes was termites, and the diet also consisted of other invertebrates and plants. My data support that of another recent study in the Northern Cape (84 km from my study site), which showed that bat-eared foxes consumed mostly Isoptera, followed by Hymenoptera and Coleoptera (Jumbam et al., 2019). Kuntzsch and Nel (1992) reported that the bat-eared foxes increased consumption of Isoptera decreased during winter and summer. Jumbam et al., (2019) showed that bat-eared foxes consumed Isoptera more during autumn and winter. My study adds to our insights on the diet of the bat-eared fox in this region by showing that even when termite numbers were low, as reflected by pitfall traps, and indirectly through the effects on aardvark physiological welfare in the same reserve (M. Phakoago, unpublished observations), bat-eared foxes were still able to source their preferred *H. mossambicus* prey. In summer when the termites accounted for less of the total diet, bat-eared foxes demonstrated increased dietary flexibility.

Further investigation is required to investigate whether the changing diet meets the energy and water demands of the bat-eared foxes. Weyer (2018), also working at Tswalu, found that *H. mossambicus* had a lower mass-specific energy content compared to *T. trinervoides* and *Anoplolepis,* ant species also eaten by aardvarks. The northern harvester termites, however, are of larger mass per individual and have a much higher water content per gram of mass compared to the other two aardvark prey items (Weyer, 2018). Unlike aardvarks, it is difficult to assess the body condition of bat-eared foxes because of their long fur. Nevertheless, from my observations, bat-eared foxes appeared to be in good body condition during my study year and breeding

was evident. The change of diet during different seasons is likely an influence of environmental conditions and invertebrate prey availability, as well as an increase of energy and water intake with increased foraging effort (Fuller et al., 2011; McKinley et al., 2018; Weyer et al., 2020). The different choice of prey during the summer may not have been a result of reduced prey availability but rather may have been a response of the bat-eared foxes to acquire sufficient water. Beetles are known to have higher energy content (21.9 J/mg) compared to termites (14.1 J/mg) (Chen et al., 2004). Termites typically have of lower mass than beetles, however, they have higher water content (77.5% of body mass) compared to the water content (60.5% of body mass) of beetles (Redford and Dorea 1984; Chen et al., 2004; Moreki and Tiroesele, 2012). In summer, water demands are likely to be much higher than in winter, and as a result, bat-eared foxes may have needed to source additional water in their diet.

The 10-fold smaller body size of bat-eared foxes (about 4 kg) compared to that of aardvarks (about 40 kg) means that bat-eared foxes need a lower absolute intake of insects to meet their energy and water needs. The aardvark, a specialist feeder, lacks the ability to maintain energy balance when preferred prey is limited or unavailable (Rey et al., 2017; Weyer et al., 2020). Aardvarks starved, with many succumbing, when there were insufficient harvester termites at Tswalu following a drought (Rey et al., 2017). Bat-eared foxes appeared to be able to find their preferred harvester termite prey even when the prey availability apparently was low. This ability may be a result of the species' sensory ability to locate its prey precisely. Foraging in groups may also provide an advantage for bat-eared foxes to find prey such as termites that does not disperse when being consumed compared to other invertebrates that may fly or disperse (Nel, 1990; Kuntzsch and Nel, 1992; Grant and Samways, 2015). The smaller size of bat-eared foxes, however, makes them more susceptible to dehydration and cold temperatures compared to a larger mammal like the aardvark (Fuller et al., 2021). Bat-eared foxes have relatively long fur that can provide some insulation compared to the almost furless skin of aardvarks (McNab, 1984). Their small size means that they also can easily access microclimates, taking refuge in burrows, holes or under bushes. The seeking of buffered microclimates as well as shifting of activity over the 24 diel cycle likely assists bat-eared foxes in reducing their energy and water demands, as shown for aardvarks (Weyer et al., 2020).

My investigation of seasonal diet change and a change of active periods in bat-eared foxes is consistent with findings of previous studies (Berry, 1981; Kok and Nel, 1992; Stuart et al., 2003; Klare et al., 2011; Périquet and le Roux, 2017 Jumbam et al., 2019). It is well established that bat-eared foxes can change their 24-h activity periods over different seasons (Lourens and Nel, 1990). The change of active periods in another myrmecophagous species, the aardvarks, to meet energy requirements obtained from invertebrate prey species (Williams et al., 1997; Weyer et al., 2020) is comparable for that for the bat-eared fox of this study. I investigated whether the active periods of bat-eared foxes varied over a year in a hyper-arid environment. As shown previously (Smithers, 1971; Nel, 1978; Koop and Velimirov, 1982; Kamler et al., 2017), active periods of bat-eared foxes differed seasonally with increased diurnal activity during winter and spring compared to other seasons. There was, however, some nocturnal activity in the early parts of the night in winter and spring, possibly reflecting the need to continue foraging to meet energy requirements during these cooler periods. When bat-eared foxes were diurnally active, foraging was much more likely to occur in the warmer late evening than in the cool mornings. In summer and autumn when globe temperatures were at the highest, diurnal activity was avoided. The lack of diurnal activity may be a response to avoid high heat loads and a subsequent risk of dehydration, or a response to changing activity patterns of prey, which may also have to avoid a high risk of desiccation in summer. Bat-eared foxes have adaptive opportunistic behaviour (Berry, 1981; Marsh, 1987; Lourens and Nel, 1990; Kuntzsch and Nel, 1992; Grant and Samways, 2015) that can be most favourable during periods of drought and decreased prey availability (de Vries et al., 2011). The adaptive opportunistic traits and ability to change diet and seasonal active periods allows them to increase nutritional intake, especially during mating season (de Vries et al., 2011) and for lactating females (Lourens and Nel, 1990; Mackie and Nel, 1989). Although not part of my systematic data collection, I observed denning and the presence of bat-eared fox pups during late spring and early summer, with pups foraging with parents outside dens from the end of January. The energetic needs of gestation and lactation, as well as restrictions of movement while denning, therefore, also may have influenced the seasonal diet of the foxes. Further study of how bat-eared foxes meet their energy demands during the energetically challenging periods of reproduction are required.

At the start of my study, I attempted to habituate bat-eared foxes to human presence, so that I could obtain much more detailed records of activity and feeding behaviour. I also attempted to trap foxes in baited cages, without success. Ideally, future studies would benefit from the use of GPS tracking collars and accelerometer loggers to provide greater seasonal activity and spatial information in the Kalahari (Cagnacci and Urbano, 2007). I also had planned to implant body temperature data loggers in the bat-eared foxes, to estimate whether their energy and water needs were met (Hetem et al., 2016). Future use of GPS tracking collars, activity loggers and body temperature data loggers could provide improved information on the feeding behaviour and activity periods of bat-eared foxes, and the influence of environmental variables on their active periods (Allan et al., 2013). Furthermore, the use of tracking collars would increase the chances of finding bat-eared foxes, allow greater observation of behaviour and scat collection (Foley and Sillero-Zubiri, 2019). As a result of the skittish and elusive behaviour of bat-eared foxes at Tswalu, scats were collected opportunistically, and I was able to collect and analyse only 82 scats. I was able to assess the seasonal diet of bat-eared foxes with a sample size (82 scats) that is relatively low, and compare the invertebrates found in the scats with invertebrates found in pitfall traps (7 months of transects).

Pitfall traps are used for sampling invertebrates that are active above-ground (Greenslade and Greenslade, 1971; Greenslade, 1973; Majer, 1987). Although they provide information about the availability of invertebrates, they are inefficient in sampling invertebrates that forage underground and flying invertebrates (Greenslade and Greenslade, 1971; Greenslade, 1973). Termites have colonies underground (Duncan and Hewitt, 1989) and the usage of pitfall traps is likely to be less successful for determining the availability of the termite species (Geerts et al., 2016). Termites move soil from underground to the surface as an activity when moving water and maintaining their nests (Turner et al., 2006; Geerts et al., 2016). The presence of fresh heaps of soil above ground can be used as an indication of activity of termites underground (Majer, 1987), and therefore should be employed in further studies to interrogate the relationship between termite presence in the environment and termites in the diet.

The impact of vegetation on the availability of invertebrates reported in this study is similar to that which has been reported previously (Weyer, 2018; W. Panaino, unpublished thesis under revision). As the Kalahari is a semi-arid environment with conditions of low rainfall and high temperatures (Parmesan et al., 2000; Holmgren et al., 2006), impacts on the availability of food resources for species are inevitable. Drought and increased air temperatures from previous years may inflict distress in ecosystems, which influences species survival (Conway, 2009; Dudney et al., 2017). The availability of invertebrates has been shown previously to alter the diet, active periods, and energy and water balance in myrmecophagous species (Weyer, 2018; W. Panaino, unpublished thesis under revision). My data showed that although the availability of invertebrate prey species was low compared to previous years of study (Figure 1.7), bat-eared foxes were able to consume their preferred prey throughout the year.

In summary, bat-eared foxes showed dietary flexibility, with harvester termites being the most utilized dietary item, but other invertebrates and plant material were also found in the scat. In summer, when bat-eared foxes had fewer termites in their scats they increased the consumption of beetles. The finding that *H. mossambicus* were consumed throughout the year, with high consumption during autumn, is similar to the results of other studies on the diet of bat-eared foxes (Kok and Nel, 1992; Stuart et al., 2003; Klare et al., 2011; Jumbam et al., 2020). I have shown that even in a year when rainfall was lower than previous years between 2015 and 2018, and invertebrate numbers in traps were low, that bat-eared foxes were able to find and still consume *H. mossambicus* during each season. The dietary flexibility of bat-eared foxes is likely to benefit them in the face of climate change, so long as increasing temperatures and a decrease of rainfall do not reduce the availability of all dietary invertebrates in the environment.

CHAPTER 5
CONCLUSION

One way to attempt to predict how organisms will respond to climate change is to assess how they respond to extreme climatic events and weather patterns that are likely to occur more often because of climate change. I took advantage of a period of low rainfall in preceding years (Figure 3.1; Panaino, unpublished data), associated with low ant and termite numbers (Weyer, 2018; Panaino, unpublished data) (Figure 1.7), in a hot semi-arid environment to investigate whether the dietary flexibility of bat-eared foxes will likely buffer them against future climate change. Rainfall and environmental temperatures are essential climatic parameters that are used for predicting future impacts of climate change on ecosystems and species (Ouhamdouch and Bahir, 2017). Over this century, surface temperatures are predicted to increase by ~4°C to 6°C in northern and southern Africa, with an increased occurrence of drought (Conway, 2006). Arid and semi-arid regions often dry more rapidly compared to mesic regions (Conway, 2006). The Kalahari, where I conducted my research, has already experienced an increase in maximum daily air temperatures, by ~0.8°C since 1993 (van de Ven et al., 2019). Within the last seven years, the Kalahari has experienced summer mean air temperatures ~3°C higher compared to the mean of the previous 35 years (Rey et al., 2018). While changes in precipitation with climate change are more difficult to predict, rainfall trends in southern Africa reveal a total decline per day of 0.003 mm over the 20th century (Jury, 2013). Similar to a previous study conducted in northern South Africa, the decreased occurrence of rainfall decreased soil moisture and surface water availability (MacFadyen et al., 2018).

The direct effects of changing precipitation and environmental temperatures because of climate change will have indirect effects for organisms, particularly by reducing food availability. In southern Africa, the growing season of vegetation has shortened because of lowered rainfall occurrence (Conway, 2006). Low rainfall and high environmental temperatures, as measured during my study year, likely influenced the growth of grass cover. Even during periods of rainfall in summer, high temperatures increase rates of evaporation and evapotranspiration (Foden et al., 2007; Jury, 2013; Eslamian et al., 2011). The timing and the frequency with which rainfall occurs can also have an impact of the growth of vegetation and diversity of species (Knaap et al., 2008; Wu et al., 2010). Indeed, the biomass and composition of vegetation is often highly susceptible to the availability of water (Barnett and Facey, 2016).

Soil moisture and vegetation growth are essential for invertebrate populations, especially invertebrate herbivores (Ayieko et al., 2010; Jamieson et al., 2012; Weyer, 2018; Nel and Hewitt, 1969). As a result of their small size, and a consequently high surface area to volume ratio, most invertebrates are highly sensitive and vulnerable to reduced moisture (Kimura et al., 1985). Their sensitivity and vulnerability to aridity often leads to decreased above-ground activity (Willmer, 1982; Berridge, 2012) during low rainfall periods, with invertebrates occupying and creating more suitable microclimates below-ground (Lees, 1943; Brust and House, 1990). Below-ground microclimates in lower soil horizons aid in reducing temperature shifts in colonies (Bale et al., 2002; Staley et al., 2007), further reducing metabolic rates, water balance and avoid heat stress (Benoit, 2010). However, some invertebrates can continue above-ground activity during periods of high environmental temperatures and water stress (Benoit, 2010). Vegetation cover and the quality of vegetation, influenced by rainfall and temperature can also influence populations of invertebrates and their activity patterns (Barnet and Facey, 2016). During autumn and winter at my arid study site, when mean grass cover was higher, I found that overall invertebrate numbers were higher than in the warmer, rainy season. A decline of invertebrates in an ecosystem may be a consequence of asynchrony of vegetation growth and timing of rainfall (Parmesan, 2006). Invertebrates, and more specifically termites, in my study area were likely more able to gain sufficient food resources when grass cover was available. However, long-term monitoring at our study site (Figure 1.7) has shown a progressive decrease in ants and termites caught in pitfall traps since 2014.

Long-term monitoring is crucial to assess how changes in temperature and rainfall influence the availability of food sources in an ecosystem. Long-term monitoring of invertebrates can provide a measure of the variation of diversity and abundance in an ecosystem (Kremen et al., 1993). Invertebrates not only are essential as food sources in an ecosystem, but they also play an important role as pollinators, recyclers of soil nutrients, and regulators of other species' populations (Kremen et al., 1993; Daily et al., 1997). A decrease of invertebrate biodiversity because of climate change may lead to altered resilience of ecosystems (Pecl et al., 2017). The invertebrate prey availability that I recorded during my study year will contribute to the long-term monitoring system that began in 2014 at Tswalu. Pitfall traps provide a general approximate availability of invertebrates, which I used to assess food sources that may influence the change

in diet of bat-eared foxes throughout the year. One limitation of pitfall traps, however, is that they only measure the general abundance of invertebrates active on the surface. Many ant and termite species at my study site had subterranean colonies, including *H. mossambicus*. Therefore, using pitfall traps to measure subterranean termite abundance can be inaccurate (Jones et al., 2005). Soil heaps can be used, as a non-invasive measure to determine activity of termites underground (Hartwig, 1965). The usage of soil cores and hand-sorting the soil, is a possible technique for estimating numbers, can be more time consuming; however, it provides a higher estimate of termite availability and therefore can be used when estimating termite availability (Jones et al., 2005). My use of pitfall traps may have underestimated the numbers of termites in the environment. Indeed, bat-eared foxes in my study were able to access and feed on termites, despite traps having very low numbers of termites. Nevertheless, long-term use of pitfall traps provides a tool to determine changing trends in the availability of invertebrate prey and relate that to vegetation and climate. Such parameters are essential when monitoring invertebrate abundance with climate change and how the trends of abundance influence species that depend and feed on invertebrates (Kwok et al., 2016). In conserving ecosystem function with climate change, it is important to determine if invertebrates are influenced by changes in vegetation or through direct effects of soil moisture (Nel and Hewitt, 1969; Stange and Ayres, 2010). Biodiversity assessments can be used to assess the diversity of species and species richness, which may improve understanding of species-specific ecological roles in an ecosystem.

Long-term measurements of soil moisture and soil temperature are factors that influence invertebrate microclimates. The investigation of soil moisture can be used to assess invertebrate dehydration tolerance and how biodiversity of invertebrates is impacted by low soil moisture (Kaspari et al., 2019). Soil moisture across different seasons can also influence the spatial distribution of vegetation (Ayal and Merkl, 1994; Kwok et al., 2016; Robinson et al., 2018), which can further impact invertebrate abundance. The variation of grass cover in my study showed an asynchronous response of invertebrate availability to vegetation cover. In some invertebrates, responses to vegetation are associated with the availability of vegetation cover, flowering, or seedling abundance (Kwok et al., 2016). Although there was no linear relationship between invertebrate abundance and grass cover, termites in pitfall traps

appeared to respond to the increase of grass during winter compared to other invertebrates. The responses of invertebrates to vegetation cover are likely influenced by flowering, soil moisture and the temperatures in ecosystems (Kok and Nel, 1992; Popic et al., 2013; Kwok et al., 2016; Duran-Bautista et al., 2020). The effects of vegetation abundance on invertebrate species are often species-specific, which also needs further study consideration (Karley et al., 2004; Letnic and Dickman, 2005).

If bat-eared foxes and other organisms within arid regions are to cope with climate change, the ecosystem will need to maintain multitrophic levels. Maintaining multitrophic levels within an ecosystem, results in increased biodiversity, energy, and nutrient flow (Wardle et al., 1997; Carignan and Villard, 2002; Soliveres et al., 2016). Monitoring of trophic levels to understand trophic cascades should comprise of studying the abundance of key species at each trophic level (Polis et al., 2000). Indicator species are essential when investigating a continuous change and the intensity of environmental stresses over long periods (Herricks and Schaeffer, 1985; Woodley, 1996; O'Connell et al., 1998; Simberloff, 1998). However, studying, and conserving indicator species may be complicated as the species may not reveal the exact set of circumstances of change and often lacks direct indication of what it is intended to indicate in an ecosystem or habitat (Herricks and Schaeffer, 1985; Simberloff, 1998). Indicator species can be used to study species richness when they are studied as an umbrella species (Shrader-Frechette and McCoy, 1993) and can also reveal alterations in an ecosystem (Landres et al., 1988; Simberloff, 1998). Conserving umbrella species that have wide home ranges will eventually contribute to preserving other species (Carignan and Villard, 2002). The preservation of indicator species or umbrella species may not entirely assist in preserving all species unless the habitat requirements of species are met (Welsh, 1990).

Termites can be considered as indicator species, ecosystem engineers and keystone species (Dangerfield et al., 1998; Jouquet et al., 2011) that often influence the ecosystems in which they live. Termites, which are the most consumed prey of bat-eared foxes, play an important role in ecosystems as natural grazers and decomposers impacting soil nutrient. Termites also impact the distribution of water in ecosystems and are key prey items for myrmecophagous species (Nel and Hewitt, 1969; Turner et al., 2006; Jouquet et al., 2011). Termites encourage vegetation growth

by increasing water infiltration through mounds (Jouquet et al., 2011). However, during droughts, increased mounds limit seed growth and ultimately vegetation growth (Watson and Gay, 1970; Watson et al., 1978). *H. mossambicus* is a termite species that does not build mounds. As natural grazers, termites often compete with large herbivores for vegetation (Nel and Hewitt, 1969), by consuming tons of grass per hectare in a year over an extensive range (Braak, 1995; Jouquet et al., 2011).

Preserving ecosystems and habitats may be well approached by the targeted conservation of species such as keystone species (Mackey et al., 1994; Simberloff, 1998). Keystone species often reflect the direct effects and relation they have on other species and the ecosystem that they inhabit (Simberloff, 1998; Carignan and Villard, 2002). Termites provide a key food resource for many animals, including the myrmecophagous mammals. Another keystone species that depends on termites, specifically *H. mossambicus,* is the aardvark. A single bat-eared fox aids in maintaining termite populations by consuming approximately 1.15 million termites per year (Stuart et al., 2003). Aardvarks provide feeding sites and create microclimates such as burrows for many other species (Pick and Mitchell, 2013) and also aid in maintaining termite populations by consuming approximately 13.5 million termites per year (Williams et al., 1997). In the absence of myrmecophagous animals, termite populations can increase and change vegetation abundance and structure in ecosystems (Jamieson et al., 2012; Jaworski and Hilszczanski, 2013; Greet et al., 2016). Changes in vegetation abundance or structure can then impact herbivore species and the interaction between herbivores and predators (Syke, 2009). Maintaining keystone species, umbrella species or indicator species increases is therefore important to limit future trophic cascades in an ecosystem from primary producers to herbivores and predators (Koh et al., 2004; Pringle et al., 2007; Glen et al., 2007; Dunn et al., 2009).

Within the Kalahari ecosystem ants and termites are the main prey for myrmecophagous species other than bat-eared foxes (Redford, 1987). As mentioned above, aardvarks feed preferentially on termites, while pangolins feed primarily on ants, but also consume termites (W. Panaino, unpublished observations). Recent research in the Kalahari has shown that drought resulted in aardvarks and pangolins starving (Rey et al., 2017; Weyer et al. 2020, W. Panaino, unpublished observations).

Aardvarks specialized on *H. mossambicus* and did not shift to eating other species when termite availability decreased (Weyer et al., 2020). Pangolins were able to change their preferred prey but the change in diet was not sufficient to meet their caloric needs (W. Panaino, unpublished observations). Previous studies have shown that bat-eared foxes were able to consume other species of invertebrates and other dietary items when their most utilized prey was limited (Kok and Nel, 1992; Klare et al., 2011, Jumbam et al., 2019). In my study when the availability of termites was low, as indexed by pitfall traps and scats of aardvarks and pangolins (M. Phakoago, unpublished observations), bat-eared foxes nevertheless consumed a high proportion of the termites. The ability of bat-eared foxes to locate and consume limited termite prey may result in interspecific competition with other myrmecophagous mammals (aardvarks and aardwolves). However, the different active periods between bat-eared foxes, aardvarks and aardwolves reduces direct competition for termites (Smithers, 1971; Williams et al., 1997; Weyer, 2018).

Increased temperature and increased aridity in the future, resulting from climate change, are likely to negatively impact the abundance of insects, increasing competition for resources. If the increased competition of resources compromises overall energy intake it will impact the physiological well-being of invertebrate predators, challenging their physiological homeostasis and fitness (Fuller et al., 2021). Often niche breadth increases when food resources decrease, enabling species to increase prey in their diet and competition for resources (Krebs, 1978; Bothma et al.,1984). However, competition for resources between sympatric species is dependent on active periods and dietary species preference (Krebs, 1978). Aardwolves, aardvarks, and bat-eared foxes consume termites; however, the preference of termites is species-specific to its myrmecophagous predator (Bothma et al., 1978; Williams et al., 1997). The three myrmecophagous predators consume different termite species, with the exception for aardvarks and bat-eared foxes. Bat-eared foxes and aardvarks forage during different active periods, which decreases competition for termite consumption between these myrmecophagous mammals (Bothma et al., 1978: Williams et al., 1997). Aardwolves eat mainly *T. trinervoides (*Williams et al., 1997; Taylor and Skinner, 2001), while both aardvarks (Weyer et al., 2020) and bat-eared foxes eat mainly *H. mossambicus.* Myrmecophagous species with overlapping diets and habitat may reduce competition through different active

periods (Bothma et al., 1978; Taylor and Skinner, 2001), although their active period will also be dependent on the activity of prey species. Both bat-eared foxes (Bothma et al., 1978) and aardvarks (Weyer et al., 2020) extend their foraging into the day when dietary items are limited. An ongoing decrease of food resources in the future because of climate change is therefore likely to increase competition.

Whether a species is a specialist or generalist feeder, climate change is likely to influence how well it copes with reduced food availability and increased competition resulting from climate change. Specialist species, which have restricted dietary flexibility, are more likely to decrease in numbers than are generalist species because of limited food resources and habitat loss (Büchi and Vuilleumier, 2014). Specialist species will have higher success in surviving when their preferred resources are abundant (Terraube et al., 2011). Generalist feeders can compensate for reduced energy from some food sources, and reduced water intake from those food items, by consuming a spectrum of available species across different seasons (Terraube et al., 2011; Jumbam et al., 2019). Bat-eared foxes in my study consumed Hymenoptera, Coleoptera and Scorpiones, as well as some Orthoptera and grubs, when their preferred prey was low (as indexed by pitfall traps). Bat-eared foxes showed a more generalist diet compared to other myrmecophagous species (Williams et al., 1997; Weyer, 2018; W. Panaino, unpublished thesis under revision), as they can consume other species apart from their preferred prey. The varied diet of the bat-eared foxes showed high intake of termites, with the appearance of a generalist diet. The diet of bat-eared foxes showed that should termite prey species decrease, the foxes will be able to consume other invertebrate prey. Such dietary flexibility has also seen in previous studies of bat-eared foxes' diet (Berry, 1981; Kuntzsch and Nel, 1992; Klare et al., 2011; Jumbam et al., 2019). The change in diet may not reflect opportunistic behaviour, but rather show preference for a species (Jumbam et al., 2019; Klare et al., 2011) that allows the bat-eared foxes to increase energy requirements compared to single species specialist (Weyer, 2018; W. Panaino, unpublished thesis under revision). Although generalist species have an advantage over specialist feeders when facing climate change, they too may be pushed to their survival limits if a variety of food resources is influenced by the changing climate. Ultimately climate change will have cascading effects across ecosystems, influencing organisms at multiple trophic levels.

Another way for animals to adjust their energetic needs in the face of insufficient food is through changing their active period (Fuller et al., 2021; Moyer-Horner et al., 2015). Animals that are normally nocturnal face high energetic demands to maintain a high body temperature during the cold night (Fuller et al., 2021). Shifting their activity to warmer parts of the day reduces the energy cost when foraging (Rey et al., 2017). Indeed, like many other mammals, bat-eared foxes in the Kalahari changed active periods across different seasons. In the colder months of autumn and winter, diurnal activity of bat-eared foxes was more common. The change in the active periods of bat-eared foxes in my study is like that shown in various other locations in South Africa (Smithers 1971; Nel 1978; Mackie 1988; Lourens and Nel, 1990). A change of active periods when food resources are insufficient can lead to shortened foraging periods to decrease the energy cost of being active, with the result of a further impact on the ability of the species to meet its caloric needs (Moyer-Horner et al., 2015). Aardwolves showed shifts in active periods during winter when their preferred species *T. trinervoides* were unavailable, but the shift resulted in shorter foraging because of short activity periods (Williams et al., 1997). Recently the use of activity data loggers in aardvarks has revealed that aardvarks shift activity to the day when there is reduced availability of resources, but the diurnal activity increased heat load on the aardvarks (Weyer, 2018). Activity shifts to the day may therefore results in mammals facing an increased thermoregulatory demand for water. Bat-eared foxes, like aardvarks (Weyer, 2018), likely rely on food intake for most of their water intake. I never observed bat-eared foxes drinking free-standing water during the year of my study. Future studies should be conducted to understand how bat-eared foxes alter their activity patterns and adjust their patterns of body temperature to cope when food resources are limited.

A tool that can be used to assess how activity patterns and body temperatures of free-living mammals vary is biologging. Biologging can help to reveal concealed data that is not evident and provides a measure that is more accurate than human observation (Block, 2009; Hetem et al., 2019). It also is a useful tool for understanding the behaviour of animals that are not easily habituated to human presence, like the bat-eared foxes I studied. Activity patterns can be recorded continuously using accelerometer loggers on collars or implanted subcutaneously on the animal's body (for example, Hetem et al., 2019). By implanting a miniature temperature-sensitive

data logger it is possible to examine whether heterothermy is exhibited when food resources are limited, as demonstrated for aardvarks (Weyer et al., 2020) and many other mammals (Hetem et al., 2016; Fuller et al., 2021). When large mammals experience energy deficits, the minimum 24h body temperature decreases, while maximum 24h body temperature increases on hot days when the mammals do not have sufficient water (Hetem et al., 2016). Body temperatures are lowered when there is decreased concentration of leptin because of lowered energy intake from limited food resources (Humpheries et al., 2003; Swoap, 2008). In arid regions where food resources are often limited, core body temperatures are lower compared to when food resources are available, even in summer (Spalton, 1999; Lourens and Nel, 1990; Hetem et al 2010). The lower body temperature is associated with a lower metabolic rate, allowing a mammal to reduce its energy expenditure (Hetem et al., 2016).

Dietary items provide most of the water for many smaller-mass animals (Williams et al., 2001; Wolf et al., 2020). However, the water and energy content of dietary items often differs between species in the diet (Redford and Dorea, 1984), which can influence the diet of a species (Wolf et al., 2020). Isoptera have an energy content that ranges between 11.6 J/mg in *T. trinervoides* to 30.3 J/mg in *H. mossambicus* and have water content that ranges between 70% to 77.5% per body mass (Redford and Dorea, 1984; Williams et al., 1997). In Coleoptera, species energy content can range between 5.2 to 20 J/mg, with water content that can range between 55% to 60% of the body mass (Redford and Dorea, 1984; Bell, 1990; Bukkens, 1997). In Hymenoptera species, the energy content ranges between 17 to 20 J/mg with water content varying between 44% to 77% per body mass (Redford and Dorea, 1984; Bell, 1990; Bukkens, 1997). Arachnida have lower energy content compared to the invertebrates that bat-eared foxes consumed in this study, with a seasonal energy average of 5.7 J/mg and water content ranging between 63% to 64% of body mass (Stewart and Martin, 1970; Norberg, 1978). Scorpiones have an energy content of 13.89 J/mg and an average water content of ~77% of body mass (Abulude et al., 2006). Energy and water content between insect adults and juvenile workers and soldiers can vary (Barker et al., 1998), which may influence the preference of adult and juvenile workers and soldiers in the diet of insect-eating mammals (Williams et al., 1997). The energy and water content of adult and juvenile workers and soldiers may also vary during different seasons (Chen et al., 2004), further affecting seasonal variation of dietary item intake of bat-

eared foxes. Understanding whether bat-eared foxes have sufficient food energy can be determined by assessing the energy and water content of their diet. Ideally, long-term monitoring studies on the energy intake of invertebrate prey species by myrmecophagous species in arid regions should be conducted to determine how invertebrate energy and water content impacted by climate change influences the energy and water intake of myrmecophagous species in regions highly affected by climate change.

Insufficient water intake resulting in dehydration, inhibits evaporative water loss, and so can be detected through elevated maximum body temperatures during the day (Fuller et al., 2021). The body water status of small mammals is dependent on the availability of food and water resources as well as the influence of environmental heat load (Xu, 1996; Kamphues, 2000; Fuller et al., 2016). Whether shifts in the diet of bat-eared foxes across seasons aided in improving water intake is not known and requires further exploration. Supplemented water supply can be beneficial for increasing water intake for species and can reduce the risk of dehydration, especially in semi-arid regions where surface water is limited (Tau, 1992; Owen-Smith and Ogutu, 2003; Hetem et al., 2016; Wolf et al., 2020). It is known that bat-eared foxes do drink when free-standing water is readily available. However, careful distribution of supplemented water, such as waterholes, is essential for preserving vegetation structure and cover (Smit et al., 2006). The distribution of supplemented water can influence animal distribution, predation (Grant et al., 2002; Dunham et al., 2004) and cause overgrazing (Farmer, 2010; Ndlovu et al., 2018). In their current environments, little is known about the thermoregulation of bat-eared foxes, and how they trade-off body temperature regulation in arid regions during water and energy deficits. Biologging of activity and body temperature would therefore be useful to assess how bat-eared foxes are impacted seasonally and how limited food resources influence their function. To better understand how climatic changes affect ecosystems and species inhabiting ecosystems, long-term monitoring systems therefore should be developed. Ideally, long-term monitoring systems should include measuring macroclimatic and microclimatic variables, vegetation, invertebrate abundance and the distribution and populations of predators that feed on the invertebrates, such as the myrmecophagous mammals.

Research is needed to not only to investigate changing macroclimates, the focus of climate change models, but also to determine the microclimates available to animals. Macroclimates influence the temperature animals experience, especially during extreme high temperatures and extreme cold temperatures (Hayward, 1965). However, most animals seek microclimates during such periods, which buffers them from the extreme macroclimates. Microclimates often provide mammals with environments that assist in maintaining optimal metabolic rates and body temperatures (Huey, 1992; Hannah et al.,2002), and can provide a mechanism to avoid hyperthermia or hypothermia (Moyer-Horner et al., 2015). The behavioural response of animals to changing ambient temperature can be monitored by observing when animals use available microclimates. Measuring the characteristics of those microclimates is important to understand how they help animals limit thermal stress and water loss. The distribution of microclimates may also influence the energy costs of animals during foraging periods and high temperatures (Hetem et al., 2019). In my study, bat-eared foxes were observed resting often outside dens and resting under shrubs during the late afternoon in summer, and in some cases basking in the sun during winter. The use of biologging to record body temperature and activity, as well as measurement of both the macroclimate and utilised microclimates, will increase our understanding of the responses bat-eared foxes to changing environmental conditions. Managing ecosystems is also important, as they provide microclimates for maintaining energy and water needs of animals, especially in arid regions (Tattersall et al.,2012).

My study on the seasonal responses of free-living bat-eared foxes, made possible by measuring black globe temperature, rainfall, average grass cover, pitfall trap prey availability, scats to assess diet, and observed activity periods has contributed to the current knowledge on how bat-eared foxes will cope in the future climate of the Kalahari, as well as other regions that become hotter and drier. Although I collected data for only one year, my study showed that bat-eared foxes in the resource-poor Kalahari possess dietary flexibility that may buffer them against some of the consequences of climate change. Further long-term measurements from bat-eared foxes, using additional tools like biologging, together with measurements of demography, population size and distribution are essential to confirm how bat-eared foxes will cope in a changed future.

Collaborative studies between scientists working in different disciplines also are important for determining how mammals will respond to future climate change. Such collaborative studies should be developed as long-term studies. The use of long-term studies will provide trends on whether ecosystems and the animals within those ecosystems are able to recover from extreme events (Howard and Dixon, 1990; Karley et al., 2004). Different methodological strategies can be used in collaborative work to better investigate and critically analyse multiple impacts on ecosystems and how to best improve ways of conserving ecosystems (Staudt et al., 2013; Lepetz et al., 2008). Ecosystem responses can be distinguished through spatial and temporal changes in vegetation, water availability, species abundance and distribution. In addition, it is important to carry out studies in various locations across a species' distribution, to improve conservation management according to their geographical area (Moyer-Horner et al., 2015). Additional studies are needed to carefully monitor bat-eared fox populations, including breeding success. One way to do so is through citizen science. Tourist and general residents in local communities can assist in increasing recorded information on bat-eared fox active periods. Records of the location and time of species' observations, such as those logged on iNaturalist, can be useful to researchers while promoting biodiversity awareness amongst the public. The use of social media records, for example through a Facebook page like Kgalagadi Sightings, can also support science and increase tourism and resultant income for protected conservation areas (Barile et al., 2017; Oteros-Rozas et al., 2017; Brandt et al., 2017; Suseno et al., 2018). In many regions, including the Kalahari, there will also be value in researchers building successful relationships with surrounding farmers, especially where they can assist reporting on the welfare of species, population distribution and active periods. As climate change is an on-going phenomenon, long-term collaborative work will increase predictive models of the consequences of climate change impacts on species physiology, trophic level functioning and -- should extinction occur – the impacts of ecosystem functioning.

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APPENDICIES

STRICTLY CONFIDENTIAL

ANIMAL RESEARCH ETHICS COMMITTEE (AREC)

CLEARANCE CERTIFICATE NO. 2019/04/21/C

APPLICANT: Ms L Molete

SCHOOL: Physiology
DEPARTMENT:
LOCATION:

PROJECT TITLE: Nutritional physiology and termal ecology of free-living bat-eared foxes (Otocyon megalotis) in a semi-arid environment

Number and Species

8X Adult male and female Bat-eared fox (Otocyon Megalotis)

Approval was given for the use of animals for the project described above at an AREC meeting held on 2019/04/30. This approval remains valid until 2021/06/02.
Unreported changes to the application may invalidate the clearance given by the AREC
An annual progress report must be provided

The use of these animals is subject to AREC guidelines for the use and care of animals, is limited to the procedures described in the application form and is subject to any additional conditions listed below:

Signed: _____ (Chairperson, AREC) Date: JUNE 3, 2019

I am satisfied that the persons listed in this application are competent to perform the procedures therein, in terms of Section 23 (1) (c) of the Veterinary and Para-Veterinary Professions Act (19 of 1982)

Signed: _____ (Registered Veterinarian) Date: 04/06/2019

cc: Supervisor: Prof A Fuller
Director: CAS

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