MYRMECOPHAGOUS MAMMALS IN A CHANGING WORLD: THE ECOLOGY OF AARDVARKS AND TEMMINCK'S PANGOLINS IN THE KALAHARI

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Of

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Declaration

Declaration with regard to independent work:

I, Makabudi Valery Phakoago, declare that this thesis is my own independent work, with the exception of where others have helped as indicated in the acknowledgements and the reference list. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. The work herein has not been submitted before for any degree or examination at any other University.

VPhakoago

_____ 12 August 2024

Signature of student **Date**

Makabudi Valery Phakoago

Dedication

This work is dedicated to the Almighty God, for all things are possible through Christ who strengthens me.

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“I can do all things (which He has called me to do) through Him who strengthens and empowers me (to fulfil His purpose-I am self-sufficient in Christ’s sufficiency; I am ready for anything and equal to anything through Him who infuses me with inner strength and confident peace)”- Philippians 4:13 (Amplified Bible). I thank the Almighty God, who gave me the strength and confidence throughout this journey.

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Abstract

Little is known about the distribution and ecology of the aardvark (*Orycteropus afer*) and Temminck's pangolin (*Smutsia temminckii*) in southern Africa as they are rarely seen and difficult to study. Both species are myrmecophagous (feed on ants and termites), primarily nocturnal, 2and they tend to be solitary. Climate change, which is resulting in hotter and drier environments in most parts of southern Africa, may affect the aardvark and Temminck's pangolin through direct impacts on the animals and through impacts on their prey resources. Understanding how climate change may impact these two myrmecophagous mammals requires us to gather further insights on how their environment and food sources are changing, how their diets overlap, how they use the environment and alter their activity to source food and buffer themselves from heat and cold, and how they are distributed across southern Africa.

Previous research conducted in the semi-arid Kalahari of southern Africa showed that a decline in ant and termite populations (as indicated by counts in pitfall traps) associated with drought resulted in starvation of aardvarks and pangolins and decreased reproductive output of pangolins. Individuals of both species starved, despite previous work indicating that the diets do not overlap, with aardvark preying predominantly on harvester termites (*Hodotermes mossambicus*) and pangolins preying predominantly on ants (mainly *Crematogaster* ants). However, the research on each species was conducted at different times, so the dietary differences may have arisen from various factors that differed between the study periods.

As part of a long-term project aimed at assessing the potential impacts of climate change on myrmecophagous mammals in the Kalahari ecosystem, the present study collected faecal samples from aardvark and Temminck's pangolin at the same time in the Kalahari for one year to compare their diets and assess dietary overlap (Chapter 3). In addition to dietary analysis, the study added to our long-term data (since September 2014) of grass cover and counts of ants and termites in pitfall traps, from September 2019 to August 2022 (Chapter 2). These long-term data revealed substantial fluctuations in grass and insect availability over time, with termite populations apparently less likely to recover after drought years compared to ants (Chapter 2). The study also assessed the abundance

and orientation of burrows that are available to the aardvark and Temminck's pangolin in the duneveld in the Kalahari during winter of 2021 (Chapter 4). Lastly, the study assessed the distribution and ecology of the aardvark and Temminck's pangolin in southern Africa using freely available images and videos from Facebook and Instagram over 10 years (2010 – 2019) (Chapter 5).

During the study, the study site, Tswalu Kalahari Reserve, experienced higher than average rainfall (2020 and 2021), resulting in high grass cover and an increase in the number of ants in pitfall traps, following a very hot and dry period in 2019. In contrast, termite numbers remained low. Despite the apparent low number of termites, as reflected in the pitfall traps, aardvark preferred termites over ants in their diet, and consumed predominantly termites of the genus *Trinervitermes* (45% of their diet) over the study period. Temminck's pangolin preferred ants over termites and consumed mainly ants of the genus *Crematogaster* (42%). Although aardvarks and Temminck's pangolin had preferences for their specific prey items, it was shown for the first time that there was dietary overlap between the two mammal species, with higher overlap when prey resources were readily available during autumn, and lower dietary overlap when prey resources were scarce during spring. The present study, however, was conducted during an unusually wet period characterized by above-average rainfall, so it is important to determine how competition for dietary items will change in hotter and drier years, when insect populations will likely be lower.

Ants and termites rely on grasses for their survival; therefore, one would predict that the abundance of burrows, dug primarily by aardvark, is likely to be related to grass cover. The present study site comprised two distinct areas, differing in grass cover as a result of differences in historical grazing pressure. I therefore investigated the availability and use of burrows in the area with low grass cover and the area with high grass cover, during winter. Burrows serve as a beneficial buffer against climatic conditions for burrowing species, offering heat avoidance during the day and warmth during the night. It was found that burrow numbers were positively associated with grass cover. More burrows also were found on the western side of the dunes than on the eastern side, most likely because the

western side receives more direct sunlight in the afternoon, providing a warmer microclimate overnight during the cold winter.

Finally, the study explored whether social media could provide supplementary information on the distribution and ecology of the aardvark and Temminck's pangolin in southern Africa. The data, which were collected through examining photos and videos on Facebook and Instagram, confirmed that the aardvark is found throughout South Africa while Temminck's pangolin is restricted to the northern regions of South Africa. The images also confirmed recent research that poor body condition is associated with greater diurnal activity for the aardvark, likely a response to high energetic demands of being active on cold nights. Little is known about drinking behaviour by the aardvark and Temminck's pangolin, with only 7 records previously published for the aardvark. It was found a further 32 records for the aardvark, and 7 for the pangolin, showing that both species do occasionally drink opportunistically. The records also provided information on the predation of both myrmecophagous mammals. Predation was observed at almost all times of the year for both species, with leopard (*Panthera pardus*) the most common predator for the aardvark, and lion (*Panthera leo*) the most common predator for Temminck's pangolin. Even though there were far fewer records of images in other southern African countries, social media appears to be a useful tool for collecting data on the distribution and ecology of the aardvark and Temminck's pangolin. Understanding the ecology and distribution of the aardvark and Temminck's pangolin in the Kalahari and other regions in relation to available prey resources and local climate is crucial for improving our conservation efforts of the species through informed management practices.

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Chapter 1: Introduction

Mammals are facing numerous threats in a changing world, including the risk of local extinction from habitat loss, climate change and illegal wildlife trade (Bowyer et al., 2019; Bennett, 2023). Studying these mammals is crucial for a comprehensive understanding of the challenges and their responses. However, some mammals such as the aardvark (*Orycteropus afer*) and Temminck's ground pangolin (*Smutsia temminckii*) are difficult to study in the wild (Ingram et al., 2019; Epps et al., 2021; Panaino et al., 2023). The aardvark and pangolin are both elusive mammals, usually solitary and nocturnal (Epps et al., 2021; Pietersen et al., 2021; Ajayi et al., 2022; Matthews et al., 2023). They play key roles in ecosystems, particularly through digging burrows and turning over soil, and feeding on insects (Haussmann et al., 2018; Chao et al., 2020; van den Bosch et al., 2023). Understanding how they respond to environmental change is essential as their decline, if it occurs, may disrupt the entire ecosystem through cascading effects.

Climate change, which is causing hotter and drier environments in much of Africa, can affect animals directly, through increased thermoregulatory demands, or indirectly, such as through the impacts on their food resources (Fuller et al., 2016). The aardvark and pangolin are myrmecophagous mammals, which feed on ants and termites. Recent research in the Kalahari, a dryland area where both species overlap, has shown that a decline in insect numbers led to starvation in both the aardvark and pangolin (Rey et al., 2017; Weyer et al., 2020, Panaino et al., 2022). Ongoing warming and drying of the Kalahari are expected to further decrease insect numbers, raising uncertainty about how the aardvark and pangolin will cope with climate change.

In order to better understand the impacts of climate change on these species, I collected data to contribute to a long-term dataset of ant and termite numbers in the Kalahari and explored how the insect numbers have changed over the long-term. I studied the diet of the aardvark and pangolin at the same time, to explore potential competition for food resources. I also assessed the abundance of burrows during winter in the Kalahari, as burrows act as important buffers against environmental extremes, and provide an indication of the distribution of pangolins and aardvarks across a landscape. Finally, I explored whether social media can be used as a tool to gain additional insights on the ecology and distribution of the aardvark and pangolin in southern Africa. In this introductory

chapter, I review climate change in southern Africa, the impact of climate change on mammals in southern Africa, provide a general overview on the aardvark and Temminck's pangolin and the potential methods that are used to monitor and study the aardvark and Temminck's pangolin. I also pose questions on how the aardvark and Temminck's pangolin will respond to the challenging environmental conditions that are expected with climate change in southern Africa.

1.1 Climate change in southern Africa

Climate change poses a significant threat to global biodiversity by disrupting ecosystem processes. Africa has already experienced an increase in extreme temperatures over the past 50 to 100 years, and predictions suggest that most regions will continue to experience further increase (Niang et al., 2014; Engelbrecht et al., 2015). Predictions indicate that temperatures in Africa will increase at twice the global rate, with a projected global temperature rise of 2 °C to 4 °C by the end of the 21st century (Niang et al., 2014; IPCC, 2023) (Figure 1.1).

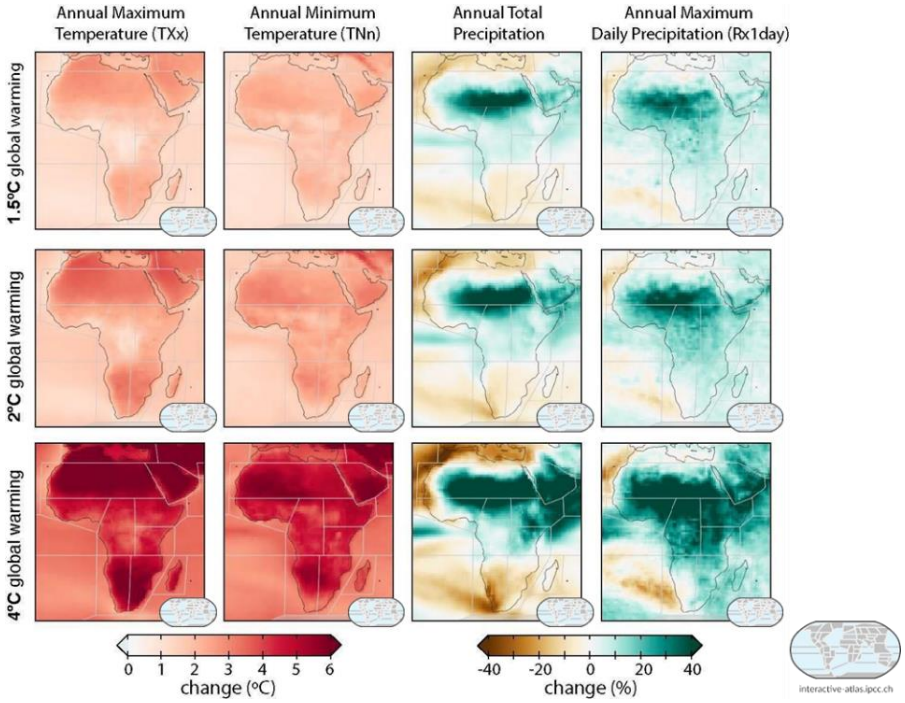

Figure 1.1: Projected changes in annual maximum temperature (TXx), annual minimum temperature (TNn), annual mean precipitation and annual maximum daily precipitation (RX1day) at 1.5 °C, 2 °C, and 4 °C of global warming (in rows) compared to 1851–1900 (IPCC, 2023).

An increase in global surface temperatures, coupled with shifting precipitation patterns, are anticipated to impact species' global distribution patterns, and potentially affect their ability to adapt and survive in situ (Lenoir and Svenning, 2015). Beyond the magnitude of these changes, the rate of climate change is a crucial factor affecting species' adaptive capacity, with rapid climatic change posing a higher risk (Loarie et al., 2009; Garcia et al., 2014).

The historical evidence in southern Africa points towards a concerning trend of rising temperatures and drying conditions across the subregion (Niang et al., 2014; Nhemachena et al., 2020). Extreme temperatures, erratic rainfall, and increasing evapotranspiration demand, along with human activities, are expected to surpass the resilience limits of ecosystems and cause irreversible landscape transformation (Ogunbode et al., 2020). These effects are particularly pronounced in southern Africa, where recent climatic changes have severely impacted various ecosystems and disrupted their services to society (Kusangaya et al., 2014, Rosendo et al., 2018). Parts of Botswana, Namibia, and South Africa would be most affected by worsening warming conditions (Figure 1.1). Recurrent droughts in the region have significantly affected ecological systems (Guo et al., 2016), including those of high conservation value. For example, increased fire intensity and frequency have led to a decline in woody biomass in African savanna woodlands, such as the Miombo woodland (Kuyah et al., 2014).

The El Niño-Southern Oscillation events further impact southern Africa, causing below-average rainfall and contributing to extreme droughts (Siderius et al., 2018). Recent years have seen intense hot droughts, with some linked to El Niño events, impacting aridity (Hulme et al., 2001; Rouault and Richard, 2005; Baudoin et al., 2017). A global phenomenon, El Niño recurs every 2–7 years with varying intensity (Siderius et al., 2018). The impact of droughts in southern Africa between 2013 and 2020 El Niño has generally been associated with effects on agriculture (Archer et al., 2017; Baudoin et al., 2017; Siderius et al., 2018; Shikwambana et al., 2022). Agriculture is the basic economic activity for most of the population in southern African countries (Siderius et al., 2018). A study on drought characteristics in the 21st century showed that El Niño caused more than 60% of the extreme drought occurrences in southern Africa (Rouault and Richard, 2005).

Concerns have been raised that the intensity and severity of droughts in southern Africa may increase in the future due to ongoing global warming, reduced soil moisture and rainfalls shifts (Shongwe et al., 2009). However, Gore et al. (2020) noted a weakening El Niño and a strengthening La Niña effect on the Walker Circulation, transitioning conditions from drier to wetter in specific years. For example, in early 2021 South Africa experienced above average rainfall and reservoirs refilled by early 2022 (Du Plessis, 2022).

Water availability is critical in hot, arid regions like southern Africa, influencing ecosystem processes and vegetation dynamics (Chown et al., 2011). Changes in temperature and rainfall can disrupt ecosystems, impact species behaviours, alter foraging, increase predation, and create advantages for some species while disadvantaging others (Wittemyer et al., 2005; Zimova et al., 2016; Visser and Gienapp, 2019; Wann et al., 2019; Pérez-Girón et al., 2020). Fluctuations in water availability can further lead to shifts in species distribution, food resources, changes in breeding success and socio-economic implications (Engelbrecht et al., 2015; Shongwe et al., 2009). For example, the earlier arrival of birds at breeding areas may not align with the abundance of their food resources (Both et al., 2009). African elephants (*Loxodonta africana*) breed year-round, but subordinate males breed during the dry season while dominant males breed during the wet season (Hufenus et al., 2018). Understanding dynamics such as these is crucial for effective conservation and management in the face of climate change and increasing water scarcity.

Drylands are so named for their arid climate, which can have a significant impact on primary productivity (Chesson et al., 2004; Brookshire and Weaver, 2015). With low precipitation, plant growth is impaired or slowed, leading to a decline in available food resources for herbivores (Chase et al., 2000). A lack of primary productivity can create trophic mismatches, where the timing of plant growth does not align with the breeding and migration patterns of herbivores (Aubry and Williams, 2022; Brown et al., 2022). As a result, herbivores may struggle to find enough food to support their populations, leading to potential declines in their numbers. The disruption in the food chain can have far-reaching consequences for the entire ecosystem, highlighting the delicate balance that exists in dryland environments.

Mammals that inhabit southern African drylands are likely to be vulnerable under the projected climate change scenarios since water is so crucial for healthy ecosystem functioning and primary productivity in arid systems (Niang et al., 2014; Engelbrecht et al., 2015). Therefore, mammals in drylands will likely be directly and indirectly impacted by the effects of climate change on their habitats and resources. The projected temperature increase together with decreased or more variable precipitation may directly affect species through increased heat stress and dehydration, as well as indirectly through impacts on primary productivity (Hoffmann et al., 2013).

1.1.1 Direct and indirect impacts of climate change on mammals

1.1.1.1 Direct impact

Mammals are susceptible to thermal stress, as their physiology is influenced by fluctuations in temperature. Extreme heat or cold can have negative effects on mammals (Buckley and Huey, 2016; Fuller et al., 2021), leading to decreased reproductive success, impaired immune function, and disrupted behavioural patterns, all of which will have follow-on effects on ecosystems (Speakman, 2008; Hetem et al., 2014; Fuller et al., 2010). In addition, heat stress can result in dehydration and organ failure (Ron and Haim, 2001; Sejian et al., 2018; Jacobs et al., 2021).

In response to high environmental temperatures, mammals rely on increased evaporative water loss to cool down their bodies (Parker and Robins, 2018; Mitchell et al., 2018). Behavioural thermoregulation is also employed, to reduce the heat load experienced. For example, shade use has the potential to reduce a mammal's radiant heat load by 50% or more (Kelly, 1950; Maia et al., 2020). In addition, some animals are likely to reduce their activity when it becomes extremely hot and may shift activity from daytime to nighttime (Hetem et al., 2012). For example, during the extreme summer heat in Saudi Arabia, the Arabian oryx (*Oryx leucoryx*) used behavioural thermoregulation to cope with thermal stress by seeking shade under trees from 06:30 in the morning, before black globe temperature exceeded their body temperature, and remained there until evening when the temperature difference became favourable for dry heat loss (Ostrowsk et al., 2003; Hetem et al., 2012). By seeking shade, Arabian oryx experienced microclimates with globe temperatures were 12 °C cooler than those in the full sun at the hottest time of the day

(Hetem et al., 2012) The behaviour also helped the Arabian oryx conserve water, saving significant amounts daily, by storing heat and then dissipating the heat non-evaporatively (Ostrowsk et al., 2003; Williams et al., 2012). Similarly, Bighorn sheep in an arid desert foraging under tree canopies or resting in caves experienced radiant temperatures 10 to 20 °C lower than if they were exposed to the sun (Cain et al., 2008).

Refuges can provide further microclimatic buffering for mammals beyond simply seeking shade. Small mammals use burrows, holes, crevices, caves, and habitats below vegetation to escape heat and cold (Cain et al., 2006; Fuller et al., 2016). For example, during cold exposure, the thermoregulatory costs for pygmy rabbits were 50% lower inside burrows than above-ground resting sites during winter (Milling et al., 2018). Using refuges allows mammals to conserve energy in cold temperatures and water in hot climates by reducing thermal gradients and evaporative water loss (van der Vinne et al., 2015), through the same mechanism as seeking shade. On top of the benefits of a cool environment, refuges are typically more humid than the outside environment (Burda et al., 2007; Whittington-Jones et al., 2011) which promotes water conservation through reduced water vapour pressure gradient between the body and the refuge thus reducing evaporative water loss (Bulova, 2002; Burda et al., 2007; Mitchell et al., 2018). However, avoidance of high ambient temperature behaviourally may restrict foraging time, and consequently food intake, which impacts survival (Sinervo et al., 2010). Nevertheless, it is crucial for mammalian populations to have access to suitable habitats that provide shelter and protection from environmental thermal stress.

Rising environmental temperatures and changes in precipitation patterns can directly alter habitat suitability for mammals. Shifts in vegetation types or loss of suitable habitats can force mammals to migrate to new areas, or result in local extinctions (Midgley and Bond, 2015; Ripple et al., 2015; Tilman et al., 2017). Changes in range or migration patterns can consequently disrupt food availability, predator-prey interactions, and overall ecosystem health. In some cases, species may be unable to adapt quickly enough to the changing climate, leading to population declines and ultimately endangering the species due to starvation, or other factors such as disease. Drought-related famine, along with diseases, have been found to be the primary cause of herbivore die-offs in drylands (Young, 1994).

During droughts in South Africa, large animals die from famine rather than from dehydration (Smit et al., 2020). Higher temperatures can expand the range of disease-carrying vectors, such as ticks and mosquitoes, increasing the likelihood of disease transmission to mammals (Halabi, 2020; McDermott, 2022). The loss of important habitats, such as wetlands, grasslands, or montane forests, can have particularly significant impacts on mammal populations that rely on these ecosystems for food and shelter.

Understanding species' responses to climate change requires an assessment of their exposure, sensitivity, and plasticity to buffer such changes (Fuller et al., 2016). With ongoing and projected climate change, an organism's ability to adjust its responses becomes increasingly critical, particularly in arid areas where animals may have already evolved some level of tolerance to natural extremes. However, uncertainties persist regarding their capacity to cope with further increases beyond pre-existing climate change experiences. Climate change and vegetation change are expected to worsen and become one of the major drivers for the loss of several wildlife species due to impacts on availability of water and forage (Dejene et al., 2023). For example, African elephants are sensitive to changes in rainfall and vegetation availability due to their body size and water requirements and may face risks from prolonged droughts and rising temperatures (Mole et al., 2016). Similarly, African wild dogs (*Lycaon pictus*), reliant on expansive landscapes for hunting and denning, are facing threats from habitat fragmentation and prey availability shifts driven by climate change (Rabaiotti et al., 2023). Recognizing the sensitivity of species such as elephants and wild dogs enables prioritizing habitat protection and management for their survival. In addition, assessing the plasticity of a mammalian species in response to climate change is essential. Some species, for example African cape buffalo (*Syncerus caffer caffer*), exhibit high adaptability, thriving in diverse habitats and adjusting their behaviour and movements in response to environmental fluctuations. Nevertheless, a severe drought in the Kruger National Park in 2016 led to the buffalo starving (Botha et al., 2023). Understanding the sensitivity and resilience of species helps us to implement interventions to support species that are less capable of coping with the challenges arising from climate change. The interventions include habitat conservation and restoration, such as establishing protected areas, wildlife corridors, and rebuilding degraded habitats.

In response to either predictable or unpredictable conditions, many endothermic mammals (Geiser and Turbill, 2009; Ruf and Geiser, 2015; Hetem et al., 2016) use heterothermy which is a physiological strategy in which animals exhibit controlled and regulated fluctuations in body temperature and allow animals to adjust their body temperature depending on environmental conditions, metabolic demands, and resource availability (Hetem et al., 2016). Heterothermy enables animals to conserve energy and water during periods of either scarcity or extreme conditions, contributing to their survival and adaptation in challenging environments (Dausmann, 2014; Hetem et al., 2016; Desforges et al., 2021; Gyhrs et al., 2022).

When animals are water-deprived, they exhibit increased heterothermy through increases in daily maximum body temperatures (Angilletta et al., 2010; Samara et al., 2012; Hetem et al., 2016; McKinley et al., 2017). Animals also may experience heterothermy through decreased 24-h minimum body temperatures, when food energy is limited (Yoda et al., 2000; Wang et al., 2006; Hetem et al., 2016). Pangolins and aardvarks displayed increased heterothermy during winter, especially in resource- scarce conditions (Weyer et al., 2020; Panaino et al., 2023), which helped in conserving water and energy. For example, aardvarks displayed minimum 24-h body temperatures as low as 24 °C, resulting in exaggerated heterothermy (Weyer et al., 2020). Similar declines in minimum 24-h body temperature have been observed in other large mammals that experienced an energy deficit (Hetem et al., 2016). For example, Arabian oryx showed low minimum 24-h body temperatures throughout the dry, resource-scarce period, irrespective of ambient temperatures (Hetem et al., 2010). However, while heterothermy may be important for survival in harsh conditions, it has been linked to decreased performance (Maloney et al., 2017). Lack of adequate energy for blue wildebeest (*Connochaetes taurinus*), in a mild environment, and Arabian sand gazelle (*Gazella subgutturosa marica*) in a hot environment, resulted in a progressive lowering of the minimum 24-h body temperature during times of heat stress on the days before death (Hetem et al., 2016). Under equivalent dehydration conditions, the red kangaroo (*Osphranter rufus*), adapted to deserts, displayed a lower degree of heterothermy compared to the eastern grey kangaroo (*Macropus giganteus*), which is adapted to more moderate environments (Dawson et al., 2007). However, the red kangaroo still managed to decrease its evaporative water loss. In

addition, rodents from Moroccan *Gerbillus spp*, reduced their energetic costs by lowering their body temperature from night time to day time observed by an average (±SD) of 8.7 (±4.2) in *G. gerbillus*, 11.1 (±3.0) in *G. amoenus*, and 7.7 (±3.3) °C in *Gerbillus* spp. (Gyhrs et al., 2022). Comisana sheep (*Ovis aries*) and Maltese goats (*Capra aegagrus hircus*) displayed decreased 24-h minimum body temperatures when food energy was limited, associated with a decreased metabolic rate (Piccione et al., 2002). Alpine ibex (*Capra ibex ibex*) also decreased energy expenditure during food shortages during winter by reducing metabolism by 60%, as evidenced by reduced heart rate, in comparison to summer conditions (Signer et al., 2011).

The ability for myrmecophagous mammals and other mammals to cope in future through behavioural and dietary shifts, as well as altered body temperature regulation, will likely depend on the extent of environmental changes. Heterothermy is a crucial survival strategy that may enable animals to thrive in harsh conditions but is likely to be associated with reduced performance (Fuller et al., 2021).

1.1.1.2 Indirect impacts

The indirect impacts of climate change on mammals extend beyond direct temperature effects, encompassing alterations in food availability (Fuller et al., 2021). For example, changes in vegetation patterns due to climate change can affect the distribution and abundance of plant species, consequently impacting the availability of food resources for herbivorous mammals (Coley, 1998; Stayver et al., 2021; Kuczyk et al., 2021). In addition, rising temperatures can cause a reduction in the availability of prey species and then have a cascading effect on animals that rely on these herbivores for food, ultimately disrupting the delicate balance of ecosystems (Melese, 2016; Grant et al., 2017). Predators and other carnivores may face declining populations as their prey become scarce, leading to further imbalances in the ecosystem (Bellard et al., 2012).

Species with a specialized diet may even face higher risks because they have fewer options to alter their diet when one source becomes unavailable due to climate change, while generalist feeders can exploit other sources (Gehring and Swihart, 2003; Pacifici et al., 2017). For example, specialist feeders such as the aardvark, pangolin, and aardwolf

(*Proteles cristata*) primarily rely on ants and termites, making them susceptible to climate change-induced shifts in the abundance of ants and termites (Pietersen and Robetson, 2023). The potential decline in the density of ants and termites not only threatens the survival of these specialized feeders but also impacts other mammals that are higher in the food pyramid. Conversely, generalist feeders such as the bat-eared fox (*Otocyon megalotis*) demonstrate dietary flexibility, allowing them to consume various vertebrates and invertebrates when preferred options are scarce (Klare et al., 2011; Jumbam et al., 2019; Molete, 2021). Thus, generalist species are most likely to be buffered when preferred food availability or prey populations become limited (Roberts and Stewart, 2018; Jumbam et al., 2019) and specialist species are likely to be pushed to alter their behaviour to find their energy requirements under climate change (Melillo et al., 2011). Although generalist species are better able to adapt to alterations in food supply, if numerous food sources are impacted by climate change, they may still be negatively impacted (McCarty, 2001; Bellard et al., 2012). In the end, ecosystems will experience cascading consequences from climate change that will affect organisms at various trophic levels (Grimm et al., 2013; Scheffers and Pecl, 2019).

1.2 Aardvark

1.2.1 Taxonomy and basic description

The aardvark (*O. afer*, order: Tubulidentata; family: Orycteropodidae) is a semi-fossorial, nocturnal mammal (Kingdon, 1971; Rahm, 1990; Taylor and Skinner, 2004; Skinner and Chimimba, 2005) with an average body mass in the Kalahari of 35 kg and a range of 29 - 42 kg (Weyer, 2018) (Figure 1.2). The aardvark was originally thought to be congeneric with either the South American anteaters (*Tamandua* spp) or pangolins, but there is no significant relationship that exists between the species, as the aardvark was ultimately taxonomically allocated to the genus *Orycteropus* (Whittington-Jones, 2006). The aardvark is related to Xenarthrans (sloths, anteaters, and armadillos) and it was only in the early 20th century when it was recognised as a distinct species, as *O. afer* in the southern African subregion (Shoshani et al., 1988; Skinner and Smither, 1990). The subspecies are poorly defined because of the variability in the morphological characteristics that were used to differentiate them (Parys et al., 2012; Taylor, 2013).

Figure 1.2: An aardvark (*Orycteropus afer*) at Tswalu Kalahari Reserve, Northern Cape province, South Africa (Photo credit: Andrea Fuller).

The body length of the aardvark is about 1.4 - 2.2 m (Shoshani et al., 1988), with a 0.6–0.7 m shoulder height and a tail length of 0.5 – 0.7 m (Kingdon, 1997). The body is pale and is sparsely haired and the legs are usually covered in darker hair (Stuart and Stuart, 2017). The long muscular tail is used for balance (Lindsey, 1999). The nose contains well developed olfactory bulbs for an excellent sense of smell (Rahm, 1990) with two vertical nares of the nostrils covered by a dense fine hair that can effectively close and act as a dust filter during feeding (Skinner and Chimimba, 2005). The aardvark has rudimentary teeth that are made of densely packed tubules composed of dentine (Knothig, 2005; Taylor and Skinner, 2004); most of the prey is swallowed without chewing (Taylor and Skinner, 2004). The aardvark possesses long claws on its four toes and powerful limbs with five toes, which it employs for its impressive digging abilities (Kingdon, 1997; Lindsey, 1999).

The sex of an aardvark cannot be distinguished by either pelage colour or morphological characteristics but requires a physical examination of the genitalia (Skinner and Chimimba, 2005). Solitary and territorial, aardvarks come together only for breeding, with little information available on their breeding behaviour (Taylor et al., 2016). In North Africa, the

breeding season is between April and May, and births occur between October and November, while in South Africa, aardvarks give birth between May and July (Kingdon, 1997). Gestation lasts approximately seven months, resulting in a singleton weighing about 2 kg (Taylor, 2013; Stuart and Stuart, 2017). The aardvark's lifespan is estimated to be around 18 years (Kingdon, 1997; Knothig, 2005).

1.2.2 Distribution

The aardvark is widely distributed across Sub-Saharan Africa (Endo et al., 2002). The species ranges all the way from Senegal to Ethiopia and South Africa but is absent from the Sahara and Namib deserts (Taylor and Skinner, 2004; Taylor and Lehmann, 2015). The aardvark is also present in the Congo Basin, although the distribution in West African rain forests is poorly known (Taylor, 2013) (Figure 1.3).

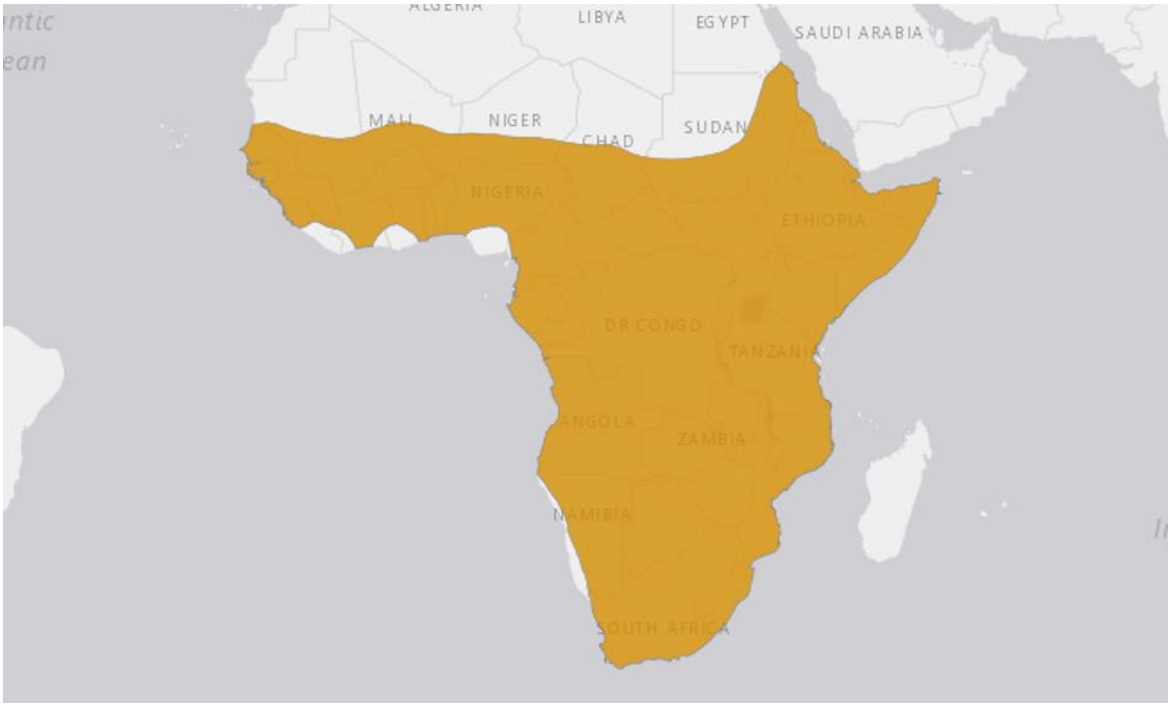

Figure 1.3: Distribution of the aardvark (*Orycteropus afer*). (Source IUCN, 2015. The IUCN Red List of Threatened Species. Version 2022-1).

In southern Africa, the aardvark is found in Namibia, Botswana, Zimbabwe, Mozambique, and South Africa (Skinner and Chimimba, 2005) with no records for Swaziland and Lesotho (Lynch, 1975; Monadjem, 1998). In South Africa, the aardvark is found throughout the

country with sightings indicating the presence of the species in all provinces (Taylor et al., 2016) (Figure 1.4).

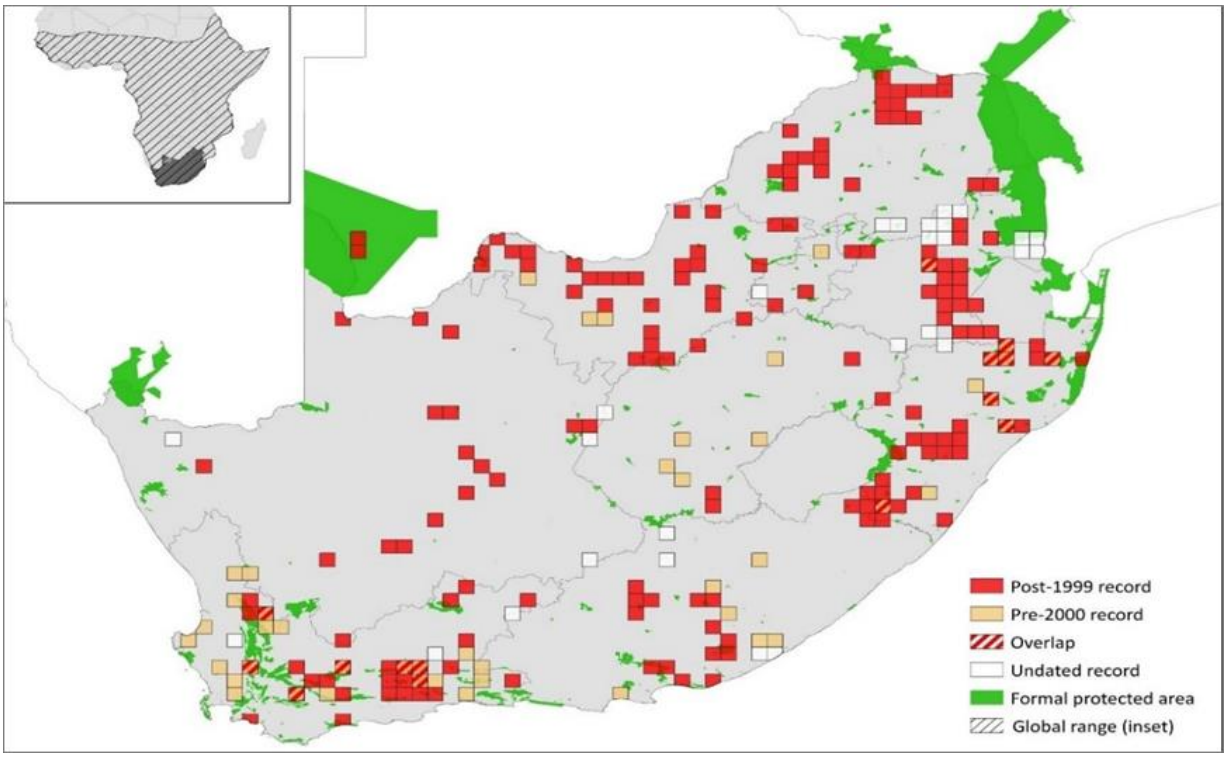

Figure 1.4: Distribution records of the aardvark (*Orycteropus afer*) within South Africa, post 1999, as per the Red List of Mammals of South Africa (Source: Taylor et al., 2016).

The aardvark's distribution is thought to be primarily influenced by the availability of suitable prey and soils conducive to burrow digging (Taylor et al., 2002; Skinner and Chimimba, 2005). Although the aardvark can be found at high elevations (Yalden et al., 1996), it is seldom observed in rocky mountainous areas where burrow construction is challenging (Taylor, 2013). In the Karoo, the presence of the aardvark is sparse, estimated at 0 - 8 individuals per 10 km^2, with uncertainty about whether the low density reflects either its true population density or the challenges of observing this secretive species (Taylor et al., 2016).

1.2.3 Habitat

The aardvark is found in a broad range of biomes (Skinner and Smithers, 1990). Its habitat includes all savanna types such as arid and semi-arid savannas in the Kalahari and Karoo

of southern Africa, open woodlands, sub-tropical thickets, farmlands, and even rainforests (van Aarde et al., 1992; Taylor and Skinner, 2004; Whittington-Jones et al., 2011; Weyer et al., 2020; Epps et al., 2021).

1.2.4 Diet

The aardvark feeds mainly on ants and termites (Melton, 1976; Taylor et al., 2002; Haussmann et al., 2018) but sometimes eats other insects such as pupae of scarabaeoid beetles or beetle larvae (Kingdon, 1971; Taylor et al., 2002). The feeding process involves the aardvark digging into colonies to capture adult ants and termites, along with their eggs and larvae, using its long, sticky tongue. The prey is then ingested and ground up by the muscular, gizzard-like stomach for digestion (Allison, 1947). The aardvark has also been observed consuming the fruit of wild cucumbers (*Cucumis humifructus*) (Melton, 1976). Diet data are available from South Africa and Uganda, through studies that have collected faecal samples to determine prey items of the aardvark (Melton 1975; Melton and Daniels 1986; Willis et al., 1992; Taylor et al., 2002, Weyer, 2018; Table 1.1).

Studies in the Kalahari and Nama Karoo in South Africa found that *Hodotermes* and *Trinervitermes* termites, and *Anoplolepis* ants, were key components of the aardvark's diet (Willis et al., 1992; Taylor et al., 2002; Weyer, 2018). In the Kalahari, *Hodotermes* termites constituted a significant portion (around 80%) of the diet during summer (Weyer, 2018). In the regions of the Karoo, *Anoplolepis* ants were the most preferred prey item during both summer and winter (Taylor et al., 2002). In Uganda, the aardvark's preferred diet was found to be *Macrotermes* termites and an unidentified ant species (Melton, 1975) (Table 1.1).

The variation in diet composition is likely influenced by the seasonal availability of different prey species in various habitats (Smithers, 1971; Smithers and Wilson, 1979; Melton and Daniels, 1986; Willis et al., 1992). Ants are typically more abundant during summer and less available during winter when they are mostly underground, leading to higher ant intake during summer and greater termite consumption during winter (Taylor et al., 2002; Panaino et al., 2022). The seasonal movements of ant species closer to the soil surface during the rainy season may also affect their accessibility to aardvarks (Swart et al., 1999). Variation

in the contributions of ants and termites to the aardvark diet across seasons and with varying resource availability, as well as during periods of low and high primary productivity, require further investigation.

The aardvark serves as a crucial ecosystem engineer, actively modifying its environment through extensive burrow digging, which exposes food from deep underground (Whittington-Jones et al., 2011; Weyer, 2018). These burrows, often exceed more than 2 m below surface and serve various purposes such as providing shelter for resting, raising young, and escaping predators (Taylor and Skinner, 2003; Whittington-Jones et al., 2011). Aardvark burrows are used by approximately 27 other vertebrate species for shelter, protection from predators, and raising offspring (Whittington-Jones et al., 2011). The burrows also function as microhabitats, offering effective thermal buffering, being warmer than the macrohabitat during winter, and cooler during summer (Taylor and Skinner, 2003; Pike and Mitchell, 2013).

Aardvarks play a role in insect control by consuming an average of about 37,000 prey items per night, totalling approximately 13.5 million prey items per year (Weyer, 2018). Importantly, the aardvark exposes insects from underground without depleting entire colonies, allowing other insect-eating mammals such as Giant pangolins (*Smutsia gigantea*), aardwolf, bat-eared fox and bird species such as ant-eating chat (*Myrmecocichla formicivora*), clapper lark (*Mirafra apiata*), cape starling (*Lamprotornis nitens*), southern yellow-billed hornbills (*Tockus leucomelas*) to take advantage of the exposed insects (Taylor and Skinner, 2002; Taylor, 2013; Stuart and Stuart, 2017). As the only prolific burrowing species in Africa, the aardvark has a unique ecological role that cannot be functionally replaced by any other African species.

Aardvark excavations significantly influence the vegetation dynamics of semi-arid environments, serving as seed germination sites and traps for plant litter and seeds (Dean and Milton, 1991; Boeken et al., 1995). The digging activity alters the soil profile, increases soil porosity, modifies soil chemistry, and enhances water infiltration, all of which contribute to maintaining plant diversity (Haussmann et al., 2018; Boeken et al., 1995; Wilby et al., 2001; Whittington-Jones, 2006). The loss of aardvarks in areas where species rely on their

burrows could have deleterious consequences for the survival of many other species (Milton and Dean, 2001; Taylor et al., 2016).

1.2.5 Behaviour and activity

The aardvark, due to its largely nocturnal and secretive habits, is challenging to observe in the wild, even during its active periods (Taylor et al., 2016; Epps et al., 2021). The aardvark exhibits a distinctive exit from its burrow before foraging, characterized by searching for potential enemies, leaping out, hopping, gazing about, and jumping around before trotting off to forage (Taylor and Skinner, 2003; Taylor et al., 2003; Mutlow and Mutlow, 2008). The primary source of prey for the aardvark comes from underground nests or mounds, necessitating extensive digging during foraging behaviour (Noirot and Darlington, 2000). The aardvark's excellent sense of smell is its key tool for locating prey items, as it doesn't rely on eyesight or hearing during foraging (Taylor, 1998).

Aardvarks have seldom been seen drinking water. Studies in semi-arid regions observed very infrequent instances of drinking water over extended periods (Taylor and Skinner, 2004; Weyer, 2018). A 12-month study conducted in the semi-arid Nama Karoo observed only two occasions of drinking water by aardvarks (Taylor and Skinner, 2004). Similarly, during a 3-year study in the Kalahari, aardvarks were never observed drinking water (Weyer, 2018). In South Africa, Kerley and Tompkins (2017) observed three episodes of drinking water by aardvarks in the eastern Karoo and one episode in the Lowveld.

While the aardvark generally remains in its burrow during the day and forages at night, recent evidence from the Kalahari suggests flexibility in behaviour and activity patterns in response to environmental fluctuations (Weyer et al., 2020). Aardvarks have been observed to switch between nocturnal and diurnal behaviour based on body condition, resource availability, and environmental conditions (Rey et al., 2017; Weyer, 2018). For example, aardvarks become diurnal during winter when resources decline and during severe droughts (Rey et al., 2017; Weyer, 2018).

Table 1.1: The aardvark (*Orycteropus afer)* diet based on studies from different regions of their distribution in sub-Saharan Africa. Table adapted from Weyer, 2020.

Author	Weyer (2018)	Taylor et al. (2002)	Willis et al. (1992)	Melton and Daniels (1986)	Melton (1975)
Study area	Tswalu Kalahari Reserve	Tussen die Riviere		Umgeni Valley	Ruwenzori
Country	South Africa	South Africa		South Africa	Uganda
Habitat	Savannah	Nama Karoo		Natal Highlands	Savanna
Aridity	Semi-arid	Semi-arid		Warm-temperate	Tropical
Annual rainfall (mm)	276	420		900	600 to 1200
Rainy season	Summer	Summer		Summer	Spring, Autumn
Main prey					
Summer	*Hodotermes* termites (~80%)	*Anoplolepis* ants	*Anoloplepis* ants (~24%) *Trinervitermes* termites(24%)	*Dorylus* ants (78%) *Odontotermes* termites (12%)	Unidentified ants *Macrotermes* termites
Winter		*Anoplolepis* ants *Trinervitermes* termites	*Anoplolepis* ants (65%) *Hodotermes* termites (11%)		Unidentified ants *Macrotermes* termites
Number of scat samples	133	350	20	5	23

1.2.6 Potential threats

The aardvark is classified as "Least Concern" by the International Union for Conservation of Nature and Natural Resources (IUCN) and not listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Taylor, 2013; Taylor and Lehmann, 2015). Despite this classification, recent studies in the Kalahari indicate a potential impact of climate change on their welfare and survival, primarily through impacts on prey abundance (Rey et al., 2017; Weyer et al., 2020). During a particularly dry and hot summer in the Kalahari, the body temperature of aardvark declined progressively to as low as 25 °C, when prey resources were diminished, ultimately leading to the death of 11 aardvarks (Rey et al., 2017). Similar die-offs during droughts in Namibia in the 1980s were reported, highlighting the vulnerability of aardvarks to changes in food availability (Wynne and Lyne, 1995).

Climate change-induced shifts in the timing of life cycle events and daily activities may affect foraging abilities, potentially leading aardvarks into areas with more predator encounters (Yang and Rudolf, 2010; Hansen et al., 2013; Ockendon et al., 2014). In cases where animals cannot move to better habitats because of fences, they may either need to compensate for low resource abundance or quality in their current environment. Increasing the time spent feeding can also increase predation risk (Metcalfe and Steele, 2001; Beauchamp, 2009; Hentley et al., 2014). In addition, aardvarks that are weak from resource-deficiency would likely be more prone to predation. Predation can occur during either day or night times when predators such as the leopard (*Panthera pardus*) are likely to select either the most vulnerable or will target the weakest prey available.

Due to human population growth and the need for land settlement and agriculture, wildlife and humans often compete for space, leading to conflict (Okello, 2005; Nyhus, 2016). The competition can result in wildlife losing habitat to agricultural expansion (Power and Verburgt, 2014; Rust et al., 2015), while increased agricultural production may also encroach on wildlife habitat (Taylor and Lehmann, 2015). On farmed areas, aardvarks create holes that can injure livestock, making them a pest that farmers want to eradicate (Power and Verburgt, 2014). In addition, aardvarks face threats from hunting for traditional medicine and bushmeat in Africa (Lindsey et al., 2013). Their body parts, such as claws,

skins, and teeth, are sold in traditional medicine markets in South Africa (Whittington-Jones et al., 2011), and their tails are considered a delicacy in Eswatini (Child et al., 2017). Despite aardvark current status, ongoing research is essential to monitor and understand how climate change impacts aardvarks and human activities on aardvark populations, ensuring effective conservation strategies for this unique species.

1.3 Temminck's pangolin

1.3.1 Taxonomy and basic description

Temminck's pangolin (*S. temminckii*, order; Pholidota, family: Manidae) (Smuts, 1832; Stuart, 1980; Gaudin et al., 2009) (Figure 1.5) is a medium-sized mammal with an average body mass of 9 – 10 kg and a range of 1 – 16 kg (Pietersen et al., 2020). A recent phylogenetic analysis suggested that Pholidota is closely related to the order Carnivora, diverging from a common ancestor approximately 87 million years ago, rather than from the ant/insect-eating order Xenarthra or the group Afrotheria as was thought previously (du Toit et al., 2014). Temminck's pangolin was previously included in the genera *Manis* and *Phataginus* but currently they are included in the genus *Smutsia* (Gaudin et al., 2009) (du toit et al., 2017; Gaubert et al., 2018).

Figure 1.5: Temminck's pangolin (*Smutsia temminckii*) at Tswalu Kalahari Reserve, Northern Cape province, South Africa. (Photo credit: Wendy Panaino).

The body length on average is between 0.72 – 0.92 m for females and 0.63 – 1.24 m for males (Skinner and Chimimba, 2005; Kaspal, 2010; Pietersen et al., 2014; Petersen et al., 2020). The pangolin is characterised by overlapping scales covering its dorsal and lateral faces, limbs, tail, and forehead, with scales ranging around 343 to 422 made of keratin (Ullmann et al., 2019; Pietersen et al., 2020). The scales are absent on the ventral side of the body, head, inner surfaces of limbs and foot pads which are covered in soft white skin (Heath, 1992; Pietersen et al., 2020). The males tend to be larger and heavier than females, with males generally weighing 10 to 50% more (Rautenbach, 1978; Heath and Coulson, 1997).

The pangolin creates burrows, either dug by itself or by other animals, for shelter. It is one of the four pangolin species found in Africa, with the other three being the giant ground pangolins, black-bellied or long-tailed pangolins (*Phataginus tetradactyla*), and three cusped or white-bellied pangolins (*Phataginus tricuspis*) (Gaudin et al., 2009; DeBeer et al., 2013; Baiyewu, 2016; IUCN, 2019) (Figure 1.6). In Asia, there are four additional pangolin species.

All pangolins are characterized by a lack of teeth and they generally use their powerful, sharp claws to access ant and termite colonies, and then lap up prey with their long mucous-coated tongue that is about 0.4 to 0.6 m in length (Kingdon, 1971; Pietersen et al., 2020; Jansen and Dalton, 2022), often longer than the head and body length combined (Mahmood et al., 2018; Baiyewu, 2016; Sulaiman et al., 2017). Temminck's pangolins have particularly poor eyesight, but an acute sense of hearing and an excellent sense of smell (Baiyewu, 2016; Pietersen et al., 2020) similar to the aardvark. The eyes are small, dark, and bulbous, with a nictitating membrane in addition to eyelids, providing protection for the pangolin from ants swarming on its head.

The lifespan of Temminck's pangolin is approximately 12 years in the wild and can extend up to 20 years in captivity (Soewu and Sodeinde, 2015). Direct field observations of their social behaviour are limited, and they are generally elusive with low population density (Wu et al., 2004; Ingram et al., 2019). The mating system involves the male and female meeting during the mating season (Pietersen et al., 2020). The female lays a scent trail,

and once located, they retire to the female's den, remaining together for up to three days, presumably mating at frequent intervals (Phakoago MV, personal observation). The gestation period ranges between 105 and 140 days, resulting in the birth of a single offspring known as a pup (Van Ee, 1978; du Toit et al, 2014; Pietersen et al., 2016).

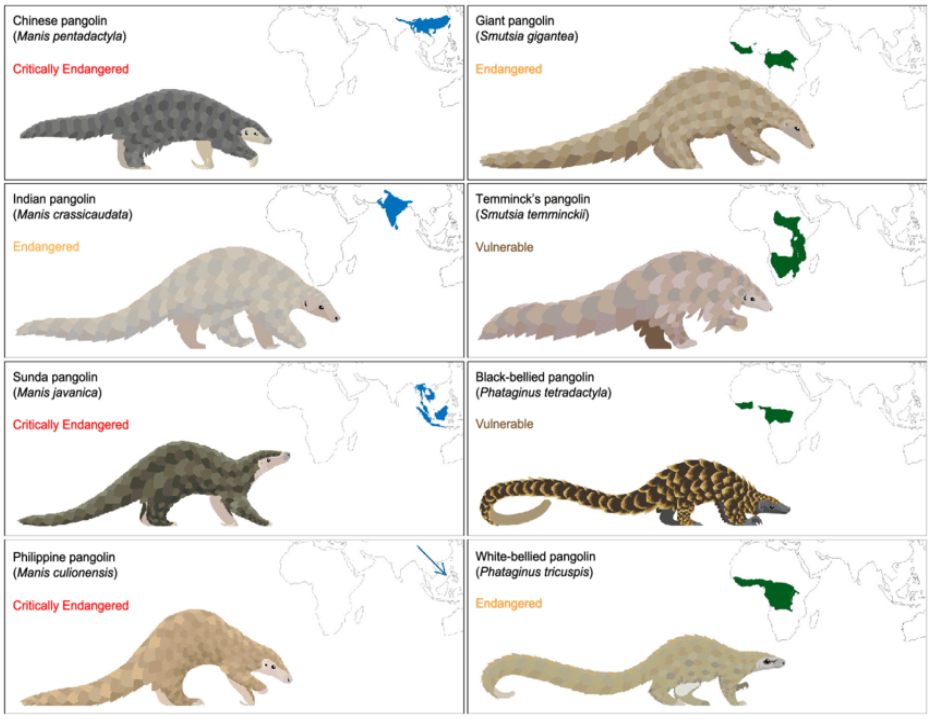

Figure 1.6: International Union for Conservation of Nature and Natural Resources Red List status and distribution of the eight extant species of pangolins. Distribution maps from the IUCN Red List of Threatened Species (IUCN, 2019) (Illustrations by Sheila McCabe).

Breeding is considered seasonal, with pups typically born during spring in regions such as the Kalahari and the old Transvaal that currently forms all or parts of Gauteng, North West, Limpopo and Mpumalanga Provinces in South Africa (Coulson, 1989; Jacobsen et al., 1991; Pietersen et al., 2020; Panaino, 2021). Pangolin mothers nurture their young in nesting burrows (Heath, 1992; Kooijman and Augustine, 2022). The pup, born with its eyes open, reaches sexual maturity at around two years (Lim and Ng, 2008; Soewu and Ayodele, 2009; Challender et al. 2012). Weaning occurs at 3 to 4 months (Lim and Ng, 2008; PCSW, 2008; Soewu and Ayodele, 2009; Challender et al., 2012). The pup's eyes are open at parturition (Swart, 2013). Newly born ground pangolin measure about 150 mm in length and weigh around 340 g (van Ee, 1966). The scales of the pup are initially soft and pale, gradually hardening in the following days (Dorji, 2017). The young pangolin

clings to its mother's tail or back during foraging trips away from the nest. At 4 to 7 months, the pup begins to forage on its own (Phakoago MV, personal observation) and when threatened, the mother rolls up her young, enclosing its head and most of the body within hers (Smithers, 1986; Pietersen et al., 2014b; Challender et al., 2019; Basin, 2023).

1.3.2 Distribution

Temminck's pangolin has the largest distribution range among the four African pangolins (Heath, 1992) (Figure 1.7). Temminck's pangolin is found in parts of southern and eastern Africa, being the only pangolin species in southern Africa and the only one adapted to arid environments. In the southern African subregion, there are records from as far as the northern parts of Chad and South Sudan, Kenya, Tanzania, Uganda, Rwanda, Angola, Zambia, and Malawi (Figure 1.7) (Skinner and Chimimba, 2005; Pietersen et al., 2016). There are also records from Botswana, Zimbabwe, Mozambique, and Namibia, except the coastal desert of Namibia (Figure 1.7) (Coulson, 1989; Skinner and Chimimba, 2005; Pietersen et al., 2016).

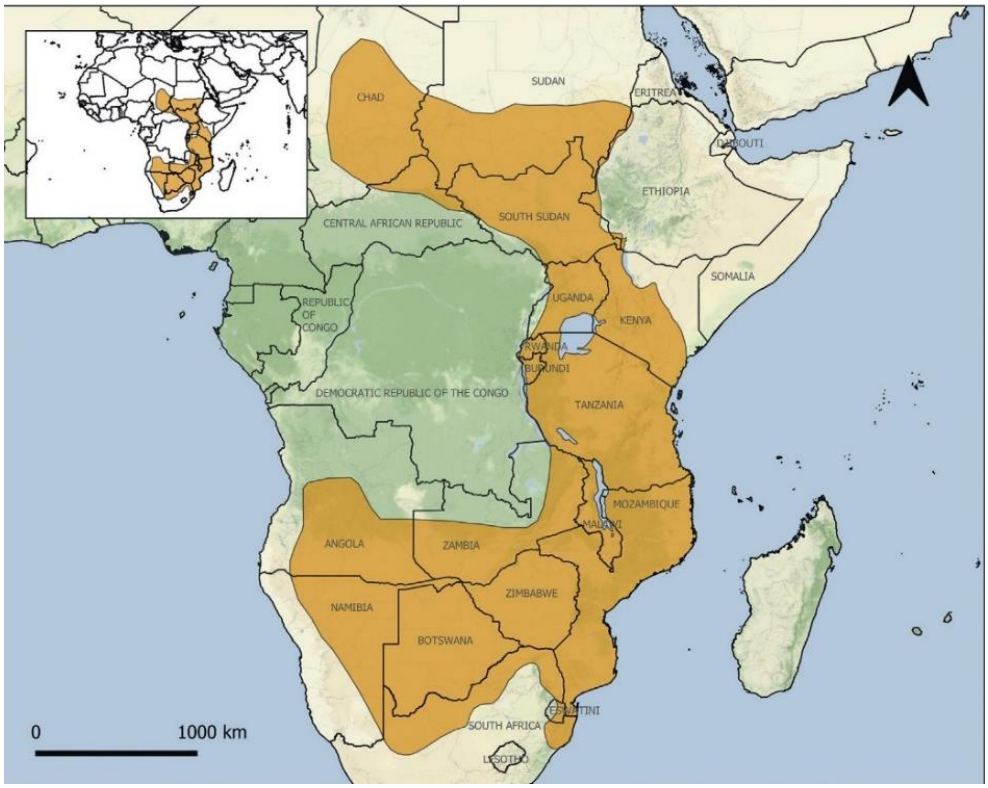

Figure 1.7: The distribution of Temminck's ground pangolin (*Smutsia temminckii*) in Africa, (Source: Pietersen et al., 2019).

In South Africa, Temminck's pangolin has been recorded in the Northern Cape, North West, Limpopo, Mpumalanga, and the northern and eastern regions of Kwa-Zulu-Natal Provinces (Pietersen et al., 2021). The species is also reintroduced in other parts of the KwaZulu-Natal Province (Figure 1.8).

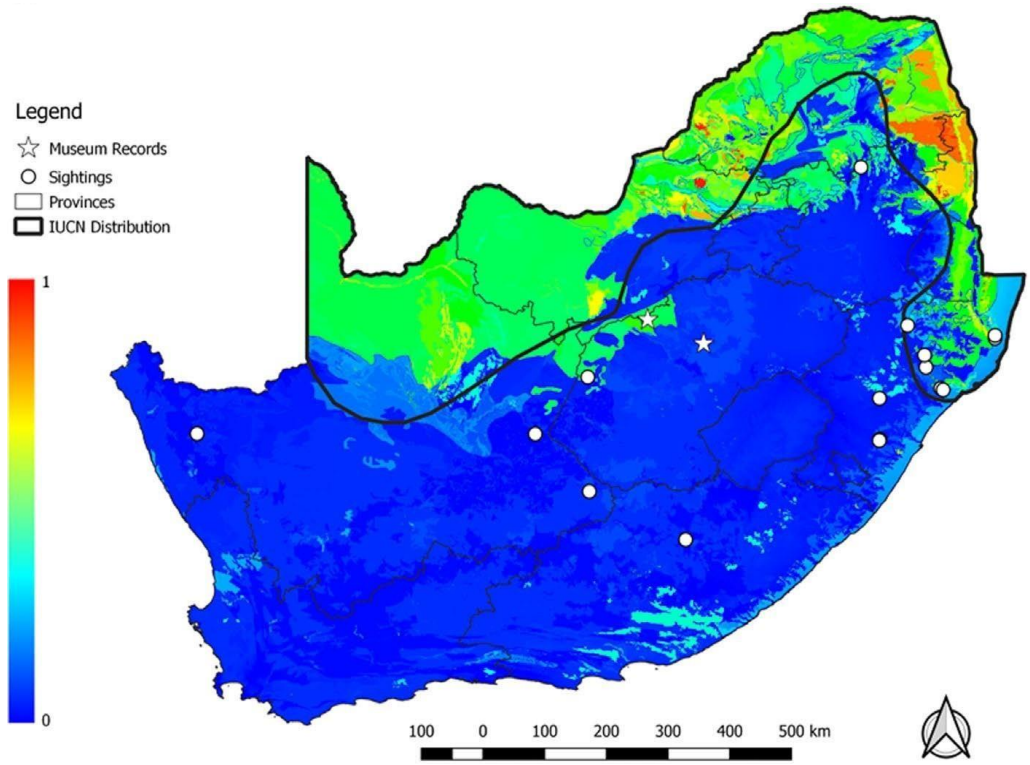

Figure 1.8: The distribution of Temminck's pangolin (*Smutsia temminckii)* in South Africa with georeferenced records. Historical (pre-2002) occurrence records, derived from museum records, and contemporary (post-2002) occurrence records, based on sightings, are depicted. The International Union for Conservation of Nature and Natural Resources distribution is indicated with a dark line (adapted from Pietersen et al., 2021).

There are also predicted occurrences in the northern part of Gauteng and the northern Free State Provinces (Pietersen et al., 2021). In the Northern Cape Province, they are mainly found in the arid environment of the Kalahari on the southwest edge of the Temminck's pangolin geographic distribution (Sweeney, 1956; Swart, 2013; Panaino, 2021; Pietersen et al., 2021).

Despite being the most widespread pangolin species and the only one found in southern Africa, there is limited research on the ecology of Temminck's pangolin. The species'

inconspicuous nature, low population densities, and nocturnal habits make it challenging to study in the wild. Most studies have focused on adult pangolins in mesic habitats, with little attention given to those in more arid and semi-arid areas (Coulson, 1989; Swart, 1996; Richer et al., 1997; Heath and Coulson, 1997; 1998; Swart et al., 1999). The lack of population estimates, and applicable research hinders efforts to determine and address the conservation needs of the species.

1.3.3 Habitat

Temminck's pangolin is well-adapted to a variety of habitats within its range. It is known to occur in arid and mesic savannas (Coulson, 1997; Panaino, 2021). The distribution of the species is closely linked to the abundant supply of prey items, primarily ants and termites (Soewu and Sodeinde, 2015; Pietersen et al., 2020). Ambient temperature also appears to influence its range, as high temperatures can reduce prey abundance and availability. The species is also found in thickets and dune veld grasslands, typically inhabiting areas with an annual rainfall ranging from 250 to 1400 mm (Skinner and Chimimba, 2005; Swart, 2013; Pietersen et al., 2019; 2020).

Temminck's pangolin avoids forested and desert areas, and it is often excluded from degraded terrains such as croplands and human settlements (Pietersen et al., 2014; 2020). The species defend territories that can range from 4 to 10 hectares, depending on the habitat. Temminck's pangolin is known to cover long distances, traveling up to 12 km per evening. Males are known to cover 32 to 81 km in 20 days (Pietersen et al., 2020).

1.3.4 Diet

Temminck's pangolin is a myrmecophagous mammal that feeds exclusively on a diet of ants and termites (Pietersen and Robertson, 2023). The diet is diverse, and pangolins consume all life stages of ants and termites, including eggs, larvae, pupae, and adults (Swart et al., 1999; Pietersen et al., 2020; Prediger, 2020). Due to the absence of teeth, they possess keratinous spines in their stomachs, functioning similarly as a bird's gizzard, to grind food (Swart et al., 1999; Botha and Gaudin, 2007). In the Kalahari, ants constitute a significant portion (90 – 95%) of pangolin diet, with termites making up the remaining 5 – 10% (Pietersen et al., 2016b; Prediger, 2020; Panaino et al., 2022). Temminck's pangolin

diet exhibits regional variation, with research consistently indicating a prey preference for specific ant and termite species rather than predominantly targeting the most abundant species throughout their distribution range (Sweeney, 1956; Richer et al., 1997; Swart et al., 1999; Pietersen et al., 2016; Panaino et al., 2022).

Previous studies that have examined the diet of Temminck's pangolin have included methods as diverse as analysis of stomach contents (Coulson, 1989), observations during foraging, and feeding behaviour (Jacobsen et al., 1991; Richer et al., 1997; Swart et al., 1999; Pietersen et al., 2016b; Prediger, 2020), direct behavioural observations, and stable isotope analyses (Sweeney, 1956; Jacobsen et al., 1991; Swart et al., 1999; Pietersen et al., 2016), and the collection of scat samples (Panaino et al., 2022). Despite the diversity in methods, the results consistently highlight a similar diet composition for Temminck's pangolin. Key prey genera, such as *Anoplolepis* ants, *Crematogaster* ants, and *Trinervitermes* termites, have been identified as significant components of their diet in South Africa, Zimbabwe, and Namibia (Swart et al., 1999; Pietersen et al., 2016a; Prediger, 2020; Panaino et al., 2022).

Previous studies on the diet of Temminck's pangolin in various habitats across southern Africa, including South Africa, Namibia, and Zimbabwe are presented in Table 1.2. These dietary assessments show that Temminck's pangolin, across diverse habitats, feeds on prey items from 19 ant and 8 termite genera (Table 1.2). The records also demonstrate a broad similarity in different assessments of the pangolin's diet. Observations from various studies in South Africa, Namibia, and other regions provide insights into their foraging habits. For example, at Tswalu in the Northen Cape province in South Africa, 603 foraging bouts were recorded by Temminck's pangolin (Panaino et al., 2022), at Kalahari Oryx Farm in the Northern Cape province, 146 foraging bouts were observed (Pietersen et al., 2016b) and 4672 foraging bouts were observed at Sabi Sand, Kruger National Park, Mpumalanga, South Africa (Swart et al., 1999). In Namibia, 156 foraging bouts were recorded in the Otjozondjupa region (Prediger, 2020). From the above-mentioned foraging bouts Temminck's pangolin was observed consuming 2-3 main prey ant genera (*Crematogaster, Anoplolepis*, and *Camponotus*) and one termite genus (*Trinervitermes*).

Table 1.2: The diet of Temminck's pangolin (*Smutsia temminckii*) based on research from different habitats (Kalahari, Savanna, Woodland), using foraging observations and prey preferences and the list of ant and termite genera that have been observed across its range and its records in each of the studies.

Author		Panaino et al. (2022)	Prediger (2020)	Pietersen et al. (2016b)	Swart et al. (1999)	Richer et al. (1997)	Jacobsen et al. (1991)	Coulson (1989)
Geographical location		South Africa	Namibia	South Africa	South Africa	Zimbabwe	South Africa	Zimbabwe
Study area		Tswalu Kalahari Reserve, South Africa	Otjozondjupa region	Kalahari Oryx Game Farm	Sabi Sand Game Reserve	The Sengwa Wildlife Research Area	Transvaal,	
Foraging observations		603	156	146	4672	2810	-	19 specimens
Prey items available	Ants	17	20	53	50		-	
	Termites	6	3	4	5	16	-	
Prey items in the diet	Ants	10	-	-	15	6	13	5
	Termites	3	-	-	5	1	3	4
Main prey items preferred	Ants	2	4	4	5	2	-	-
	Termites	1	2	1	1	1	-	-
Genera recorded in the diet including main and those observed being preyed on								
Ant genera		1,2,3,4,5,6,7,8,9	1,2,3,4,5, 8	1,2,3,	1,2,3,4,5,8,9,10, 11,14,18	2,3,5,10	1, 2, 3, 5,8,10, 11,12,13,14,15,16	2,3,17,19
Dominant prey genera in pitfalls		*Monomorium*	*Monomorium*	*Pheidole*	*Pheidole*			
Dominant prey genera in the diet		*Crematogaster* (~55%)	*Anoplolepis* (48%)	*Anoplolepis* (~48%)	*Anoplolepis* (77%)	*Anoplolepis*		
Termite genera		a,b,c	a,e,h,	a	a,b,d,h		a,d,e,f,g,h	a,d,e,h

Ant genera: *[1]Crematogaster, [2]Anoplolepis, [3]Camponotus, [4]Tetramorium [5]Pheidole, [6]Tapinolepis, [7]Lepisiota, [8]Monomorium, [9]Ocymyrmex, [10]Myrmicaria, [11]Polyrhachis, [12]Acantholepis,[13]Tapenonia, [14]Aenictus, [15]Technimyrmex, [16]Xiphomyrmex, [17]Paltothyreus, [18]Dorylus,[19]Formicidae.* ***Termite genera:*** *[a]Trinervitermes, [b]Hodotermes, [c]Psammotermes, [o]Odontotermes, [e]Macrotermes, [f] Alyscotermes, [g]Rhadinotermes, [h]Termitidae.*

Various studies on the diet of Temminck's pangolin across different regions have shown consistent patterns of dietary preference. Despite the availability of a wide range of ant and termite genera in their habitats, pangolins primarily consume a limited selection of ant and termite species. For example, studies in the Kalahari identified 17 ant and 6 termite genera and in Namibia 20 ant and 3 termite genera were available to pangolins, but pangolins predominantly fed on a small subset of these species. Similar findings were observed in the Sabi Sands and other areas, where pangolins exhibited a preference for specific ant and termite species despite a higher abundance of other prey items (Coulson, 1989; Jacobsen et al., 1991; Richer et al., 1997; Swart et al., 1999). These consistent dietary patterns suggest a strong selective feeding behaviour in Temminck's pangolins across different geographical locations (Table 1.2).

Studies across different regions have consistently shown that pangolins prefer less abundant prey items. For example, even when *Monomorium* ants. was the most abundant genus in two study areas, it made up less than 1% of the diet, while *Crematogaster* (55%) and *Anoplolepis* ants (48%) were the most preyed upon genera in the diet of Temminck's pangolin (Prediger, 2020; Panaino et al., 2022). Similarly, *Pheidole* was the most widespread genus in certain studies and contributed only about 1% to the diet of Temminck's pangolin. In contrast, the genus *Anoplolepis* played a more significant role, contributing 48% (Pietersen et al., 2016b) and 77% (Swart et al., 1999) to the overall diet of Temminck's pangolin. These findings highlight the selective foraging habits of pangolins, suggesting that factors beyond prey abundance, such as prey accessibility, behavioural characteristics, or nutritional content, may influence their dietary choices.

In various studies, the genus *Anoplolepis* consistently dominated the diet of Temminck's pangolin, indicating a strong preference for this ant genus. The selectivity might be influenced by factors such as soil surface conditions and rainfall, as *Anoplolepis* becomes more abundant during rainy seasons (Panaino et al., 2022). The activity of ants is largely influenced by temperature and relative humidity (Prins, 1982). The worker ants forage from their nest searching for food (Slingsby, 2017). During cold seasons, the activity of *Anoplolepis* is lower during winter than summer (Addison and Samways, 2000). Behavioural observations and dietary studies underscore the importance of *Anoplolepis*

ants in determining the distribution and diet of Temminck's pangolin in the southern African subregion (Swart et al., 1999; Pietersen et al., 2016b; Pietersen et al., 2020).

Crematogaster ants are prevalent on the bases of tree trunks rather than on the ground (Tschinkel, 2002; Santini et al., 2011) in the Kalahari, and are known for their slow movement, making them accessible to Temminck's pangolin through small nest entrances. The pangolin employs its claws to break these entrances and use its sticky tongue to gain access to the nests, showcasing adaptive feeding strategies (Panaino et al., 2022).

While behavioural observations provide valuable insights into the main prey species, scat samples offer a non-intrusive and comprehensive record of the animal's diet, capturing both common and less common prey items (Kelly et al., 2012). In addition to the main ant and termite genera mentioned earlier, various other members of ant and termite genera have been identified in the diet of Temminck's pangolin, further enriching our knowledge of their foraging habits (Table 1.2). Other ant genera reported to be consumed by Temminck's pangolin in southern Africa include *Tetramorium, Tapinolepis, Lepisiota, Ocymyrmex, Myrmicaria, Polyrhachis, Acantholepis, Tapenonia, Aenictus, Technomyrmex, Xiphomyrmex, Paltothyreus, Dorylus* and unidentified ant of the family Formicidae. In addition, various termite genera that have been recorded to be consumed by Temminck's pangolin in southern Africa include *Hodotermes, Psammotermes, Odontotermes, Macrotermes, Alyscotermes, Rhadinotermes*, and unidentified termites of the family Termitidae (Table 1.2).

Pangolins play an ecological role as predators of ants and termites, as creators of burrows, and as prey species (Chao et al., 2020). By foraging on ants and termites, pangolins regulate the populations of these insects (Challender et al. 2014a; Baiyewu, 2016; Chao et al., 2020). It is estimated that an individual pangolin consumes approximately 70 million ants and termites per year, providing a service to other animals that feed on plants that are targeted by these insects (Hua et al., 2015). Previous studies on pangolins recorded more than 26 000 prey items in the stomach, of which 97% comprised of ants (Lee et al., 2017). Similar observations were estimated in their stomach contents of a Sunda pangolin (*Manis javanica*) to include more than 200 000 ants in a day (Harrison, 1961; Shi and Wang,

1985). Temminck's pangolin is recorded to consume an average of 15 400 ants and termites per 24-h and estimated to consume ~5.6 million ants per year (Panaino et al., 2022). The potential consequences of the absence of pangolins could cause trophic cascades.

Temminck's pangolin has a slow reproduction rate and low population density, producing either one offspring (Coulson, 1989; Pietersen et al., 2020; Panaino, 2021) once every two years (Pietersen et al., 2020). The slow reproductive rate means that pangolins do not reproduce rapidly to replenish their populations in the face of threats such as habitat loss, poaching, and other environmental pressures which makes it challenging for pangolin populations to recover quickly if they face declines. In addition, the low population densities of pangolins mean that they are not typically found in large numbers across their range. They tend to have relatively large home ranges for foraging and may not encounter conspecifics frequently, further limiting opportunities for breeding and population growth. In contrast, insect populations have a shorter generation time than other animals (Horn, 2000; Sharma, 2014). While insect populations can recover quickly, the populations of pangolins may not rebound as rapidly. The potential consequences include an abundance of insects leading to habitat deterioration, crop damage, reduced grass growth, and productivity (Averensky et al., 2010), resulting in soil erosion (Kairis et al., 2015). The decline of vegetation can, in turn, affect the entire food chain as herbivores rely on vegetation for food, and predators that prey on herbivores will also be negatively impacted.

Pangolins, as burrowing mammals, act as ecosystem engineers, contributing to a healthier ecosystem. Their burrowing activities involve turning over the soil, aerating it, and spreading nutrients, enhancing soil quality and mineralization (Chao et al., 2020; Rodgers et al., 2017). In addition, pangolin burrows serve various ecological purposes to other species, providing shelter for raising young and escaping from predators. In Anamalai Hills, India, species such as the Travancore tortoise (*Indotestudo travancorica*) use the burrows of the Indian pangolin (*Manis crassicaudata*) (Deepak et al., 2016), whereas in Dja Biosphere Reserve, Cameroon, pouched rats (*Cricetomys emimi*) and the African bush-tailed porcupines (*Atherurus africanus*) were camera-trapped going in and out of the burrow of active giant ground pangolin on the same evening, and the porcupine was

photographed within 15 minutes after giant ground pangolin activity (Bruce et al., 2018b; Hoffmann et al., 2020). These burrows also serve as thermal refuges, maintaining stable temperatures throughout the day and insulating inhabitants from external ambient temperature fluctuations (Bao et al., 2013). During burrow digging, pangolins impact several soil processes, including the turnover of organic matter and mineralization (Rodgers et al., 2017; Chao et al., 2020).

Pangolins also act as bioturbators, contributing to soil destratification (Chao et al., 2020). Pangolins' ecological role as natural pest controllers and soil caretakers is highly significant, and conservation efforts aimed at protecting them would yield positive environmental dividends (Challender et al., 2014). The foraging behaviour of pangolins, particularly Temminck's pangolin, benefits other insect-eating mammals. While digging up ants and termites, Temminck's pangolin does not deplete entire colonies, but leaves behind exposed ants and termites that other animals can exploit. Birds such as ant-eating chats, chat flycatchers (*Bradornis infuscatus*), and cape starlings were frequently observed following Temminck's pangolin in the afternoon, taking advantage of the exposed ant and termite colonies for feeding (Phakoago MV, personal observation).

Temminck's pangolin faces few natural predators, but reports indicate instances of predation by lions (*Panthera leo*), leopards, spotted hyenas (*Crocuta crocuta*), honey badgers (*Mellivora capensis*), and Nile crocodile (*Crocodylus niloticus*) (Coulson, 1989; Pietersen et al., 2020; Jansen and Dalton, 2022). Predation events primarily involve younger and more vulnerable individuals, with honey badgers demonstrating skill in tackling and consuming pangolins (Swart, 2013; Panaino W, personal observation). When threatened, a pangolin adopts a defensive posture by curling up into an almost impenetrable ball, with forelimbs grasping hind limbs and its powerful tail curled around its body, effectively protecting its vulnerable stomach, head, and limbs (Chao et al., 2020; Pietersen et al., 2020). Pangolins also play a role as host species of endo and ecto-parasites, bacteria, protozoans, viruses, ticks, and pentastomes (Wicker et al., 2020). Overall, in the absence of pangolins and other myrmecophagous mammals, the whole ecosystem will be negatively affected, from more insect populations to damaged soil quality and reduced plant productivity.

1.3.4.1 Dietary overlap

A variety of prey items that are available to myrmecophagous mammals have been reported (Redford, 1987). Despite the variety, there is some dietary overlap between myrmecophagous mammals that occurs when ants and termites become limited and when ants and termites become abundant (Schoener, 1982; Pietersen and Robertson, 2023). Dietary overlap occurs when two or more species consume the same type of food resources (Colwell and Futuyma, 1971) and does not necessarily mean competition is taking place, especially if food is abundant (Whitfield et al., 2013). In some cases, dietary overlap may be reduced through mechanisms such as niche partitioning where species divide available food resources in either space or time to minimize competition (MacArthur and Levins, 1967, Chesson, 2000, Salsamendi et al., 2012).

Niche partitioning is one of the main mechanisms that limit interspecific competition between species (Schoener, 1974; Kent and Sherry, 2020). Consequently, studies on dietary overlap are important for understanding community structure and the coexistence of ecologically similar species (Orłowski and Karg, 2013, Arrizabalaga- Escudero et al., 2018, Bosenbecker and Bugoni, 2020). However, optimal foraging theory (MacArthur and Pianka, 1966; Schoener, 1971) predicts that dietary niche breadth will increase as the availability of high-quality resources decreases, such that animals may broaden their dietary niche to include a wider variety of other prey items when resource quality declines, including those that may not be as optimal but are still viable sources of energy to avoid competition (Stephens et al., 2019; Greene et al., 2020). A broader foraging strategy may allow for more efficient energy acquisition in times of scarcity, helping individuals to maintain their energy balance and increase their overall chances of survival and reproduction (Sahoo, 2012; Srinivasu et al., 2018; Greene et al., 2020).

1.3.5 Behaviour and activity

Temminck's pangolin is predominantly nocturnal but is also diurnal and crepuscular and activity may vary according to season, prey availability and to avoid predation (Swart, 1996; Pietersen et al., 2014; Panaino et al., 2022). The species exhibits seasonal variation in activity, being nocturnal during summer and diurnal during winter in the Kalahari, by avoiding extreme daytime temperatures and extremely cold night time temperatures

(Pietersen et al., 2014; Panaino, 2021). When not active, Temminck's pangolin spends most of its time resting in burrows. The mean daily duration of activity has been recorded to be 5.7 ± 2.0 hours in the Kalahari, with no seasonal variation, while in the lowveld, it has been recorded to be 3.9 ± 1.9 hours, ranging from 0.6 to 8.3 hours (Swart, 1996; Pietersen et al., 2014). Active time is correlated with feeding intensity and is considered a response to difficulty in accessing prey, especially during winter nights when ants are less active and congregating deeper in their nest chambers (Pietersen et al., 2014; 2016a).

The species displays unique foraging behaviours, such as following a zigzag path covering a large area within feeding sites and using their well-developed olfactory senses to locate prey beneath the soil surface (Swart, 1996; Swart, 2013). The foraging behaviour of Temminck's pangolin involves covering varying distances in search of food, influenced by prey preferences that change with season and rainfall (Swart, 2013; Panaino et al., 2022). In South Africa, males have been observed covering up to 3.8 km per night, while females cover approximately 2.2 km, and this activity takes about 4 to 6 hours of foraging time, depending on the season (Pietersen et al., 2020; Phakoago MV, personal observation). Although only a smaller portion of their time is dedicated to feeding, estimates range from 7 to 20%, depending on the environment, with most of the active time spent foraging, especially in dense bushes or vegetation (Richer et al., 1997; Swart et al., 1999).

Feeding bouts in Temminck's pangolin are typically short, lasting around 40 seconds, and may be terminated in response to the insects' defensive mechanisms (Swart et al., 1999). Although Temminck's pangolin is rarely seen drinking free-standing water, it will drink opportunistically, obtaining most of its body water through prey consumption (Pietersen et al., 2020; Panaino, 2021). The adaptability of Temminck's pangolin to different habitats and its ability to cover considerable distances contribute to its success in diverse environments.

1.3.6 Potential threats

All pangolin species, including Temminck's pangolin, face severe threats primarily arising from poaching for local and illicit international trade, making them the most illegally traded mammals globally (Challender et al., 2015; Heinrich et al., 2016; IUCN, 2019). Temminck's

pangolin is listed as Vulnerable on the IUCN Red List, with an estimated population reduction of 30 to 40% over the next 27 years (Petersen et al. 2014). Global estimates indicate that nearly 900,000 pangolins were trafficked between 2000 and 2019 (Challender et al., 2020). The demand for pangolin body parts, especially scales contribute to the decline of Temminck's pangolin. Scales are sought after for traditional medicine purposes, despite lacking scientific evidence of their efficacy (Swart, 2013; Pietersen et al., 2014; Jansen and Dalton, 2022).

In addition, pangolins are hunted for bushmeat (Mahakata and Ndlovu, 2022), considered a delicacy in some cultures, consumed as wild meat in West and Central Africa (Challender et al., 2015; Ingram et al., 2019) and consumed as a luxury in southern Africa (Zimbabwe) (Soewu and Sodeinde, 2015; Sheperd et al., 2017). More specifically, in Benin pangolins are used as food sources (Akpona et al., 2008). In addition, despite being fully protected by national laws pangolins were among the most desired types of bushmeat in Cameroon with nearly half of pangolin consumers willing to pay more for a pangolin meal than for other meat in local bushmeat markets and restaurants (Walsh, 2020; Nguyen et al., 2021). Anadu et al. (1988) found that white- and black-bellied pangolins, grouped together as tree pangolins, ranked eighth among the mammals that consumers in southwestern Nigeria most preferred.

Another threat to pangolins, in particular ground pangolin, is mortality related to electrified fences (Stracquadanio et al., 2024). Out of 14 recorded taxa, pangolins were the second most reported killed by fences, with ground-level electrified fences having a larger negative impact than other fence types (Stracquadanio et al., 2024). Electrocution by electrified fences in conservation areas poses a serious hazard, causing 2 to 13% of Temminck's pangolin mortality (Beck, 2010; Pietersen et al., 2014; 2016; 2020; Panaino et al., 2022). Researchers estimate between 400 and 1 000 Temminck's pangolin are electrocuted each year in South Africa (Pietersen et al., 2020; Jansen and Dalto, 2022). The electrocution occurs when a pangolin approaches the bottom strand of an electrified fence to cross and the strand strikes its sensitive underbelly (Pietersen et al., 2020; Pietersen, 2022). After being shocked, the pangolin rolls into a ball around the wire and is shocked repeatedly until it succumbs to the electrocution (Pietersen et al., 2016; Pietersen et al., 2020; Jansen

and Dalton, 2022). Other threats include habitat loss, road mortalities, and land degradation to further threaten the species (Ngwenya, 2001; Pietersen et al. 2014; Pietersen et al., 2016a).

Predicted increases in global temperatures due to climate change may lead to significant impacts on the geographic range of all pangolin species. For example, the research that has been done on Temminck's pangolin in the Kalahari highlights the negative impact of climate change on their welfare, specifically the decline in prey abundance due to changing climatic conditions. Rising temperatures and shifting rainfall patterns are altering Kalahari vegetation, resulting in reduced ant and termite populations, which are vital food sources for these pangolins. Consequently, the distribution of Temminck's pangolin is expected to be severely impacted by these changes (Panaino, 2021; Pietersen and Challender, 2020). Urgent conservation efforts are crucial to protect this vulnerable species and ensure its continued existence in the wild.

1.4 Potential methods to monitor and study the aardvark and Temminck's pangolin

The monitoring of rare and elusive mammal populations such as the aardvark and Temminck's pangolin, poses significant challenges for conservation efforts. Developing accurate methods to estimate population abundance or density is crucial for managing threatened species (Harris and Yalden, 2004; Zero et al., 2013). Due to their shy, solitary behaviour and occurrence in densely vegetated habitats, and occurring at naturally low population densities, aardvarks and pangolins are difficult to find and study. Monitoring efforts are required as the species are potentially facing various threats. Despite being less threatened according to the International Union for Conservation of Nature and Natural Resources in the case of the aardvark, and threatened in the case of pangolins, there is a lack of standardised survey methods to detect and assess the population numbers of both species.

Various direct and indirect methods have been employed with mixed success for monitoring elusive species (Ingram et al., 2019). The methods include direct sighting surveys (Dorji, 2017; Ingram et al., 2019), telemetry (Pietersen, 2013; Weyer, 2018;

Willcox et al., 2019; Panaino, 2021) burrow counts (Akrim et al., 2017; Ingram et al., 2019), line transects (Buckland et al., 1993; Stober et al., 2017; Ingram et al., 2019) camera traps (Bruce et al., 2018a; Hart et al., 2022), citizen science (Anton et al., 2018; Farhadinia et al., 2018), and social media (Di Minin and Hausmann, 2020). Another method used is the monitoring of animals' tracks, which has been a fundamental aspect of ecological research, providing valuable insights into the movement patterns, and habitat preferences of various species (Katzner and Arlettaz, 2020). The study of animal tracks also has the potential to yield significant palaeobiological and palaeoenvironmental interpretations (Falkingham et al., 2020) Recent advancements in tracking technology have further transformed the field of animal ecology, enabling researchers to observe animal movement and behaviour in unprecedented detail (Trappes, 2023). Each method has its advantages and limitations, and there is a need for standardised and robust approaches to assist conservation practitioners in accurately assessing population numbers and trends.

1.4.1 Direct sighting survey

The direct sighting survey is a method in which the surveyor observes and counts each animal directly; they can be carried out in a variety of ways, such as transects, plots, and trail surveys; and can be carried out during the day or at night (Ingram et al., 2019). Direct sighting surveys provide a straightforward way to collect data on animal presence and abundance in each area (Meehan et al., 2017). However, they may be influenced by factors such as surveyor expertise, weather conditions, and the behaviour of the animals being observed (Meehan et al., 2017). Despite these potential limitations, direct sighting surveys remain a valuable tool in wildlife monitoring and conservation efforts (Meehan et al., 2017; Ingram et al., 2019).

1.4.2 Burrow counts

Identifying and counting burrows can be conducted either along transects or through quadrat/plot-based surveys, assessing whether the burrows are active by looking for fresh footprints, recent claw marks, or signs of recent activity such as tracks close to the burrow (Subba, 2021; Ingram et al., 2019; Stracquadanio, 2023). Burrow counts have been the primary method used in surveys to evaluate the status and distribution of elusive species, providing insights into burrow density across various habitat types (Wu et al., 2004;

Bhandari and Chalise, 2014; Thapa et al., 2014; Dorji, 2017; Katuwal et al., 2017; IUCN SSC Pangolin Specialist Group, 2018). However, accurately assessing the status and distribution of aardvarks and pangolins through burrow counts relies heavily on the surveyor's ability to distinguish between resting burrows, feeding digs, and active versus inactive burrows (Vleck, 1979; Taylor and Skinner, 2004; Whittington-Jones et al., 2011; Weyer et al., 2020). The absence of validation methods such as camera-traps may lead to overestimates of the abundance of a species, compounded by the variability in criteria for identifying burrows across regions (Meehan et al., 2017). In addition, using burrow counts to infer habitat preferences may be flawed due to variation in detection across different habitats and potential biases introduced by hunting pressure (Lettink and Seddon, 2007; Burton et al., 2015). Coarse-scale monitoring of burrow density can still offer insights into species presence and status over time, particularly in ground-dwelling species inhabiting open habitats. Nevertheless, confirming burrow occupancy through additional methods like camera-trapping is crucial for accurate assessments, given the complexity of burrow structures and the potential for multiple species to use or create burrows.

1.4.3 Radio telemetry

Radio telemetry technology has evolved significantly since its inception in the 1960s, offering precise monitoring of wild animals' behaviour and ecology through methods such as Very High Frequency tracking transmitters, satellite, and Global Positioning System (GPS) tracking (Cochran and Lord, 1963). The technology remotely collects data on animal movement, behaviour, habitat preference, and physiology aiding in understanding the resource selection and ecological parameters. Radio telemetry has facilitated the collection of animal location data with impressive precision (Thurfjell et al., 2014), a fundamental assumption being that tagged animal do not significantly differ behaviourally from untagged animals. The Very High Frequency transmitters, which operate within the frequency ranges of 148– 174 MHz and 215–235 MHz, are cost-effective and versatile (Manville et al., 2024). They are employed in a range of device models, including collar-mounted units, ear-tag or tail mount attachments, feather harnesses, fin insertions, and surgical implants (Naef- Daenzer et al., 2005; Tozetti and Martins, 2007; Lu et al., 2021; Cornelsen et al., 2022; Robinson et al., 2023).

Radio telemetry units, facilitated by the transmitters, come in various sizes and masses (Naef-Daenzer et al., 2005; Makuya and Schradin, 2023), and should be used for animals for which the transmitter is less than 5% of the animal's body mass (Brooks et al., 2008; O'Mara et al., 2014; Coetsee et al., 2016; Makuya and Schradin, 2023). Transmitters with sufficient signal range suitable for external use across a wide spectrum are available for species as small as hummingbirds and bats, to large mammals (Lu et al., 2021; Cornelsen et al., 2022; Robinson et al., 2023). Transmitters can range in mass from ~0.2 g to 3.3 g for use in small mammals (Griffin et al., 2020; Makuya and Schradin, 2023), to ~5 g to 120 g for medium-size mammals (Lim and Ng, 2008; Pietersen et al., 2014; Schoppe and Alvarado, 2015; Sun et al., 2019) and more than 300 g in medium to large mammals (Weyer et al., 2020). Battery life can extend from only 10 days in small devices but can exceed 3 years with larger batteries (Gregersen et al., 2023; Manville et al., 2024). The Very High Frequency transmitters are also used in animals such as snakes, sea otters (*Enhydra lutris)*, sharks, sea and terrestrial terrapins, and tuna for research and tracking purposes (Jepsen et al., 2002; Seber and Schofield, 2019; Manville et al., 2024). In addition to being relatively lightweight, transmitters and their means of attachment need not be bulky, so that they do not impede regular movement and behaviour of the study animal (Robinson et al., 2023). Collar variation equipped with external antennas can conserve battery life by activating a "sleep mode" and some set ups may include supplementary (global positioning system) units, introducing an additional frequency for tracking (Manville et al., 2024). Prices per unit also vary depending on size and the supplier, and the cost is often factored into grants as a major budgeting item, as these devices are crucial for gathering data to understand basic ecological parameters of animals.

Despite its universal use and effectiveness, radiotelemetry requires the live capture of animals and the attachment of tracking devices that remotely return spatially explicit locations, at pre-set intervals. The method can be intrusive (Arnemo et al., 2006; Cattet et al., 2008; Ponjoan et al., 2008). For example, in pangolin studies, transmitters are affixed to dorsal scales to track movement and assess home range (Swart, 2013; Pietersen et al., 2014; Panaino et al., 2023) and in the case of aardvarks they are sometimes immobilised and inserted with tracking transmitters (Rey et al., 2014; Wilcox et al., 2019; Weyer et al.,

2020); aardvark are not tolerant of collars and telemeters cannot be attached externally. While radio telemetry facilitates data collection in remote areas, its implementation involves risks such as capture stress and myopathy in immobilised animals using anaesthetic drugs, requiring specialised permits and veterinary support. Another challenge is that sometimes the transmitter does not last more than three months due to high transmitter drop-off rates (Lim and Ng, 2008; Panjang, 2012; Nash et al., 2018). Although radio telemetry is currently playing a great role in collecting data from remote areas, where it is difficult to cover physically, and contribute for conservation of biodiversity, it is expensive and requires substantial funding.

1.4.4 Line transects

Line transect sampling is often used to estimate animal densities in ecological studies. However, obtaining accurate density estimates using this method can be challenging due to various factors such as imperfect detection, incomplete coverage of the study area, and variability in animal behaviour particularly with inconspicuous and rarely seen species, making it time-consuming and inefficient for estimating population densities (Timock and Vaughan, 2002; Mathai et al., 2013). Visibility varies among different locations, and the ability to detect a species can vary between sites, impacting detection rates, especially for species that are not highly visible (Denis et al., 2017). These challenges can lead to biases and uncertainties in the data, making it difficult to achieve precise density estimates from line transects alone. However, distance sampling techniques are useful when studying burrow-using species, to enhance detection accuracy during ecological surveys (Sollmann et al., 2016). Measuring the distance from the observer to the detected object, such as the entrance of a burrow, can provide more accurate information about the animal's presence or activity leading to more reliable population estimates and ecological assessments for burrow-dwelling species (Castellón et al., 2015; Schlacher et al., 2016). Animals that inhabit burrows, such as rodents, Cape ground squirrels (*Xerus inauris*), meerkats (*Suricata suricatta*) or burrowing reptiles, tend to concentrate their activities around their burrow systems making it more likely to detect them near their burrows during surveys (Shrader et al., 2008; Strandburg-Peshkin et al., 2020). While useful for ground-dwelling species or areas suspected of high population densities, density estimates based on the line transects require additional ecological information and are limited to habitats where

signs along transect are detectable. Factors such as season and substrate type must also be considered as they affect both density and detectability. In addition, the accuracy of density estimates from line transects is sometimes compromised due to poor environmental conditions and insufficient data availability. Occupancy sampling based on transect surveys and counts of pangolin burrows for example or other verifiable signs may be feasible, but grid cell size and survey times must be guided by ecological knowledge that is currently lacking for most elusive species (Buckland et al., 1993; Ingram et al., 2019). Direct observations for occupancy sampling would be impractical due to the nocturnal nature of most aardvarks and pangolins, limiting observations to human-made pathways in forested or vegetation areas where detection frequency would be too low for this method to be viable.

1.4.5 Camera traps

Camera traps represent a technological method that can offer an effective means to survey species that are challenging to locate (Burton et al., 2015). Camera traps have become increasingly popular as a low-cost option for monitoring the ecology and distribution of various species. In comparison to traditional survey methods, camera traps can expedite the detection process, detecting activity patterns within a population and correlating these patterns with landscape features and environmental temperature (Hanya et al., 2018; Bouroş et al., 2019). Camera traps have gained traction, particularly in monitoring elusive species, and they are less intrusive than line transects that often require designated paths for surveying (O'Connell et al., 2011; Ingram et al., 2019). While the use of camera traps can vary in terms of sampling strategy and intensity (Khwaja et al., 2019), it has been reported that employing camera traps in general activity surveys as part of biodiversity monitoring, located along trails, can result in low detection rates (Willcox et al., 2019). Nevertheless, camera traps provide valuable insights into the timing of animal emergence and return (Pietersen, 2013; Weyer, 2018; Panaino, 2021). Camera traps can also be used to target potential signs, such as ant nests or burrows because placing camera traps near areas suspected to have ant nests or burrows, researchers can capture images or videos of animals interacting with these features of the landscape (Bruce et al., 2018a, b).

1.4.6 Social media and citizen science

In the past decade, the rapid growth of information available on social media and citizen science initiatives has transformed how people learn and connect globally (Brundidge, 2010; Bela et al., 2016; Roth-Cohen and Avidar, 2022). Social media platforms, such as Facebook, Instagram, and Twitter, have become primary sources of online public information, facilitating interaction, sharing daily activities for billions of individuals worldwide (Zafarani et al., 2014; Preece, 2016). Citizen science platforms like iNaturalist leverage the power of crowd sourcing to engage people in scientific research and data collection to allow individuals to contribute to research projects ranging from astronomy to zoology, empowering them to participate actively in the scientific process (Dickinson et al., 2012). The widespread use of smartphones equipped with high-resolution cameras, internet connectivity, and Global Positioning Systems has made it easier to gather valuable data on social media and citizen science contributing to conservation science (Di Minin et al., 2015; Sullivan et al., 2019).

The rise of social media is influencing the global status of wildlife (Martin et al., 2018), offering new advantages and opportunities for information gathering and monitoring vulnerable species at risk of extinction. Social media records can serve as an additional tool alongside traditional monitoring methods, such as observations and camera trap surveys (Hausmann et al., 2018; Di Minin and Hausmann, 2020). Users may share images and associated soft data, including species identification to gather insights into the distribution and ecology of specific species (Zhang et al., 2012; Barve, 2014). The use of social media, with its efficient and cost-effective approach, engages with conservation hotspots and allows wildlife researchers to virtually cover more ground and access data from non-surveyed locations (Tulloch et al., 2013; Hausmann et al., 2018; Di Mini and Hausmann, 2020).

Social media is particularly beneficial for elusive or cryptic species that are challenging to monitor across their range (Pietersen et al., 2014; Taylor et al., 2016; Hausmann et al., 2018; Sullivan et al., 2019; Di Minin et al., 2020). The aardvark and Temminck's pangolin serve as excellent models for the application of social media in conservation sciences. Although rarely seen, these mammals are charismatic and attractive to social media users

and the public. The current population trends for both mammals are unknown, but in a world where information is increasingly available online through social media platforms, details such as date, location, behaviour, size, and sex of an animal can be obtained (Sullivan et al., 2019). Tools such as hashtags, geo-tags, and keyword identifiers make social media posts easy to search and filter, allowing conservation scientists to mine specific data related to a species or location and gain additional insights into wildlife distribution, conservation, and management (Kim et al., 2016).

Citizen science involves the public in scientific research for a large-scale collection of data across various locations and time periods (Chandler et al., 2017). The approach can be particularly useful for studying elusive mammals as it harnesses the power of community involvement to gather information over extensive geographic areas, helping researchers to collect data that would otherwise be challenging to collect. However, this approach has limitations, as errors have been found on a site like iNaturalist, impacting data quality. Providing citizen scientists with the appropriate tools and knowledge on species can maximize data quality and enhance the effectiveness of the approach (Ellwood et al., 2017). Data from citizen science are often perceived as unreliable due to the difficulties in effectively identifying a species (McKelvey et al., 2008). For example, species such as aardvark and pangolin are sometimes identified wrongly on platforms like iNaturalist. There are also relatively few records. Data collected in non-systematic formats such as those derived from citizen scientists have also been criticized for being opportunistic, having presence data with low resolution, and being spatially and/or temporally auto- correlated (Elith and Leathwick, 2007; Stockwell and Peterson, 2002; Yackulic et al., 2013).

Despite these limitations, data collected via citizen science have been effectively used in both marine (Richardson et al., 2012; Eastman et al., 2014) and terrestrial ecosystems (Creel and Creel, 2002; McCaffrey et al., 2005; Kosmala et al., 2016). These studies show that data from citizen science can be useful for evaluating a variety of questions across the broad field of animal ecology and are particularly applicable to scenarios where systematic surveys are either impractical or expensive to conduct (Cohn, 2008; Dickinson et al., 2012).

Citizen science remains a valuable technique to study the ecology of endangered species that covers extensive areas, such as certain bird species that migrate across continents (Cooper et al., 2015; Kobori et al., 2016), whales that undertake extensive migrations in oceans (Tonachella et al., 2012; Bruce et al., 2014; Lodi and Tardin, 2018; Kelly et al., 2020), and large mammals that roam over savannas (Dickinson et al. 2010; Ward et al., 2015; Brown and Williams, 2019). Its efficacy and precision in modelling resource use and selection will, however, depend on the study, the species, the way the data were collected, thoroughness in validating the data, and use of clear and well described protocols, the questions to be addressed, the landscape characteristics, the relative availability, accessibility and road network within the different habitat types (Quinn, 1995). In addition, involving the public in data-hungry projects is important to cover extensive ground in less time (Buesching et al., 2015), and to provide baseline data to guide management action (Ward et al., 2015). Involving the society also increases their understanding of environmental issues which is essential in conservation and environmental protection globally (Reed, 2008; Bonney et al., 2009; Silvertown, 2009).

1.5 Problem statement and rationale for present study

The aardvark and Temminck's pangolin face potential challenges in the changing climate of the Kalahari. The region is experiencing increasing heat and aridity, leading to a decline in prey abundance. Previous studies have raised concerns about the future survival of both mammalian species due to a potential increase in competition for declining food resources. While previous individual studies on the diet of aardvarks and pangolins in the Kalahari indicated no overlap, these studies were conducted at different times, making it challenging to draw generalized conclusions. In addition, possible fluctuations in ant and termite populations over time, for which we have little data, may impact the welfare on pangolins and aardvarks. My research is aimed at addressing these gaps by simultaneously assessing the extent to which aardvarks and Temminck's pangolins rely on ants and termites as prey and investigating long-term changes in their likely prey abundance. The impact of increasing environmental temperatures on both species is not well understood, and burrows, which serve as critical thermal refuges, are also essential for these mammals. We know very little about the density and locations of the burrows. As such, I assessed the distribution and use of burrows during winter. Lastly, not much is known

about the ecology and distribution of the aardvark and Temminck’s pangolin from southern Africa. I therefore used social media records on Facebook and Instagram to gather information on their distribution and ecology.

The scarcity of accurate population data for aardvarks and Temminck's pangolins in the wild poses a challenge for assessing their conservation status, despite their International Union for Conservation of Nature and Natural Resources Red List categorizations. Aardvarks, identified as keystone species, contribute significantly to ecosystems by providing burrows that serve as refuges for various other species. As the sole prolific burrowing species in Africa, the unique role played by aardvarks cannot be easily replaced by other African species. Conversely, Temminck's pangolins face a dire situation as the most traded mammal species globally. Despite being categorised as Vulnerable; little is known about their ecological role within ecosystems. To better comprehend the ecological importance of aardvarks and pangolins, empirical data on their ecology is crucial. Aardvarks, with their burrow-providing behaviour, and pangolins, facing threats like electrocution, require detailed investigations into their distribution, dietary preferences, and burrow use. Such data can enhance our understanding of how these species navigate arid environments, offering valuable insights for their conservation, especially concerning climate change.

Understanding the ecology of these species is vital for conservation efforts, especially given the limited data on their population numbers and the threats they face from activities such as illegal wildlife trade and electrocution by electrified fences. By collecting data on their distribution, dietary preferences, and burrow use, I aimed to improve our understanding of their survival in an arid environment and contribute to projections for their sustainability under climate change. The study will also enhance our knowledge of mammal responses to environmental changes and inform effective conservation planning and management strategies in southern Africa, ultimately promoting biodiversity preservation and ecosystem health in the face of ongoing climate change.

1.6 Aims and objectives of the study

1.6.1 Aims

The overall aim of the study was to investigate the ecology of two myrmecophagous mammals (aardvark and pangolin) in the Kalahari region of South Africa. The study also collected additional data from southern Africa using social media images of aardvark and Temminck's pangolin to further understand the ecology of the species. The investigation involved comprehensive data collection from the Kalahari, incorporating long-term assessments of vegetation and insect availability. Tracking of tagged pangolins was carried out to gain insights into their prey selection patterns. Faecal samples were collected from both Temminck's pangolins and aardvarks for dietary analysis, facilitating a comparison of their respective diets. The study included aardvarks, which were opportunistically observed and followed when spotted, as they were not subjected to tagging. The study also investigated the use of burrows and orientation of the burrows in the dune field.

1.6.2 Objectives of the study

- Assess long-term patterns of grass cover, and ants and termites in the Kalahari between 2014 and 2022.
- Investigate prey preference and dietary overlap of the aardvark and Temminck's pangolin at the same time in the same environment.
- Assess the abundance and orientation of burrows that are available to aardvark and pangolin in a dunefield in the Kalahari and
- Investigate how much information is available on social media about the aardvark and Temminck's pangolin, and to gather valuable information on their distribution and ecology in southern Africa.

1.7 The Kalahari region of South Africa

The Kalahari region of South Africa is located primarily in the Northern Cape province in South Africa and extends into Botswana and Namibia (van Rooyen and van Rooyen, 1998; Mthombeni, 2019). The Kalahari is semi-arid to arid region with vast sandy savannas, red dunes, and sparse vegetation, including grasses, acacia trees, and succulents (van Rooyen and van Rooyen, 1998; Nash, 2015). The climate of the Kalahari is characterised

by high air temperatures during summer and low air temperatures in winter (below freezing on occasion), with low and unpredictable summer rainfall (van Rooyen and Bredenkamp, 1996; Tyson and Crimp, 1998; Schulze, 2003). Mean annual rainfall is ~325 mm (ranging between 175 and 595 mm) (van Rooyen and van Rooyen, 2017). Evaporation rates are very high in summer months and can exceed precipitation by six-fold (Williamson et al., 1988; Tyson and Crimp, 1998).

Despite the harsh climate, with a wide daily range of air temperature, and infrequent summer thunderstorms, the Kalahari supports a diverse range of wildlife, including small, medium to large mammals (Paniw et al., 2019; van der Weyde et al., 2020; Fuller et al., 2021; Deacon et al., 2024). The region includes the Kgalagadi Transfrontier Park, renowned for its wildlife and natural beauty, attracting tourists interested in safari tours and cultural experiences (Tichaawa and Lekgau, 2020; 2024). While the Kalahari contributes to the local economy through limited agriculture and rich mineral resources, it faces significant challenges, including that of climate change. The southern Kalahari within western South Africa has been identified as a climate change “hot spot” (de Sherbinin, 2014). Kalahari species, although adapted to hot and dry conditions, may be particularly vulnerable to further heat and aridity projected with climate change (Rey et al., 2017; Paniw et al., 2019; Boyers et al., 2021; Fuller et al., 2021).

1.8 Research questions

- How has grass cover score, ant and termite population numbers in the study area change over time and is there a correlation between changes in grass cover score and the abundance of ants and termites in the study area between 2014 and 2022?
- What are the main prey items preferred by aardvarks and Temminck’s pangolins and what extent do the diets overlap in the study area?
- Are burrows found more in high grass cover areas than low grass cover areas, what is the abundance of burrows (dunes and flats) available to aardvarks and pangolins and which orientation of the burrows do they prefer the most in the study area?
- Does social media provide a useful data on the distribution and ecology of aardvarks and Temminck’s pangolins?

1.9 Thesis outline

Chapter 2 assessed the long-term patterns of grass cover, ants, and termites in the Kalahari from 2014 to 2022, within changing climatic conditions. Through transects and pitfall traps, I showed that low rainfall between 2017 and 2020 led to reduced grass cover, while high rainfall in 2021 resulted in significant grass recovery. The ant and termite populations showed an overall decline over time, although ant numbers recovered following heavy rains. These findings highlight the complex relationships between climate, vegetation, and insect population dynamics, offering critical insights into how these organisms may respond to future climatic shifts in the Kalahari ecosystem. Changes in prey species abundance may in turn impact species such as the aardvark and Temminck's pangolin. The chapter highlights the need for better knowledge in predicting future ecological responses, informing conservation strategies, and enhancing our understanding of dryland ecosystem resilience.

Chapter 3 investigated the dietary preferences and overlap between aardvarks and Temminck's pangolins in the Kalahari through simultaneous analysis of faecal samples and measurement of prey abundance using pitfall traps, over one year between September 2020 and August 2021. I found that aardvarks predominantly consumed *Trinervitermes* termites during spring and summer and consumed *Hodotermes* termites during autumn and winter, while pangolins predominantly fed on *Crematogaster* ants during spring and winter and consumed *Anoplolepis* ants during summer and autumn. Despite both mammals showing clear prey preferences, there was significant dietary overlap during resource-abundant periods (summer and autumn) and less overlap during scarce periods (winter and spring), suggesting reduced competition and possible niche partitioning. The study highlighted the need for further research across varying climatic conditions to fully understand these dynamics. The chapter provided insights into how Temminck's pangolins and aardvarks coexist and use resources and highlighted the potential impact of climate change on prey abundance and feeding behaviour.

Chapter 4 assessed the abundance, location and orientation of burrows available to aardvarks and pangolins at Tswalu Kalahari Reserve, highlighting the roles that burrows play in providing favourable microclimatic conditions. From 61 transects covering 7.6 km²

during winter, I identified 260 burrows with most burrows found in areas with high grass cover than low grass cover. Burrows were found more on dunes compared to dune streets and were mainly located on the western side of north-south running dunes. Tagged pangolins showed a preference for burrows on dunes and on the western side of dunes. I also measured microclimatic conditions and found that burrow temperatures were more stable than outside temperatures and provided cooler environment during the day, particularly in west-facing burrows. These findings highlight the ecological importance of burrows in helping mammals buffer extreme temperature fluctuations in the Kalahari.

Chapter 5 explores how social media can be used as a tool to gather information on the elusive aardvark and Temminck's ground pangolin, focusing on their distribution and ecological behaviours. By collecting photographs and videos of aardvarks and ground pangolins posted on Facebook and Instagram between 2010 and 2019, I uncovered new insights into their distribution patterns, activity levels, drinking behaviour, and predation. I also confirmed that aardvarks are more active during the day when in poor body condition, suggesting a behavioural response to their physical state. Social media is a user-friendly tool to gather additional data and has the potential to be used for gathering insights from other elusive mammals.

Chapter 6 provides the thesis conclusions, including the potential responses of mammals to climate change, based on my findings of the responses of two myrmecophagous mammals in the Kalahari region. The conclusion chapter also highlights the implications for conservation and management and recommendations for future research.

1.10 Ethical clearance and research permits

The study was approved by the Animal Research Ethics Committee (AREC) of the University of the Witwatersrand (Ethics clearance number 2020/09/06/C) and the Tswalu Foundation. The Provincial permits to conduct research in the Northern Cape were obtained from the Department of Agriculture, Environmental Affairs, Rural Development and Land Reform (Permit numbers: FAUNA 2018-2022 (0838/2018), (0839/2018) and FAUNA (0530/2021), (0529/2021).

Chapter 2 – Long term patterns of grass cover and ants and termites in the Kalahari

2.1 Introduction

Climate change is widely recognised as one of the most significant threats to global biodiversity (Román-Palacios et al., 2020; Mezel and Fedmeyer, 2021). Climate change directly affects insects, which are ectothermic organisms that rely on external conditions to reach their active body temperature (Bale et al., 2002; Filazzola et al., 2021). While some insects are conformers and solely depend on internal processes, others actively seek microclimates that will raise their body temperature and metabolism using external sources of heat (Clopton, 2007; Abram et al., 2017). High environmental temperatures, which are occurring more often and to a greater extent with climate change, can lead to dangerously high body temperature and dehydration in insects, affecting their survival and reproduction (Abram et al., 2017; O'Sullivan et al., 2017; Filazzola et al., 2021). Climate change may also affect insects indirectly through changes in the vegetation on which insects depend (Oliveira et al., 2011; Menta and Remelli, 2020). For example, the growth of grasses in dryland environments is closely linked to precipitation. Drought causes reduced grass productivity, leading to a decline in insect numbers (Weyer, 2018; Palmquist et al., 2021). Changes in temperature and precipitation patterns can also disrupt the key timing of events, leading to reduced reproductive success for grasses and insects (Renner and Zohner, 2018; Chen et al., 2019).

Insects perform numerous roles in ecosystems, not only as food sources, but also as predators (biocontrol of pest species), recyclers of soil nutrients, and as pollinators (Wills and Landis, 2018; Elizalde et al., 2020). A decrease in insect biodiversity associated with climate change may lead to an altered resilience of ecosystems (Pecl et al., 2017), with pronounced impacts on specialized feeders. Myrmecophagous animals, such as Temminck's pangolin, the aardvark, bat-eared fox and the aardwolf feed primarily on ants and termites (de Vries, 2013; Pietersen and Robertson, 2023). A decline in these insect numbers, or a change in their availability or distribution (Rey et al., 2017; Chao et al., 2020; Epps et al., 2021), may result in starvation for these myrmecophagous animals (Rey et al., 2017; Weyer et al., 2020; Panaino et al., 2022). Some myrmecophagous animals may alter their foraging behaviours to find sufficient food if their usual insect prey become less available or more difficult to locate (Swart et al., 1999; de Vreis, 2013), for example, by increasing foraging time or shifting their diet to other species. Aardvarks in the semi-arid

Kalahari became more diurnal in response to reduced prey abundance, but did not change their diet, and many individuals died of starvation (Rey et al., 2017; Weyer et al., 2020).

While concerns have been raised about the impact of climate change on insects (Pareek et al., 2017; Halsch et al., 2021; Menzel and Feldmeyer, 2021; Parr et al., 2022; Harvey et al., 2023), there are few long-term datasets that allow us to determine how insect populations are being impacted. I investigated how has grass cover score, ant and termite population numbers in the study area changed over time and if there was a correlation between changes in grass cover score and the abundance of ants and termites in the study area between 2014 and 2022. I therefore contributed to data collection and analysed a dataset of grass cover, and ant and termite counts in pitfall traps, over 8 years in the Kalahari region of South Africa. I also examined specifically how the ants and termites, previously reported to be the key prey items for Temminck's pangolin and aardvark, namely *Crematogaster* and *Anoplolepis* ants, and *Trinervitermes* and *Hodotermes* termites, changed in their numbers over time. Understanding the responses of grass cover, ants, and termites to variation in climate will allow us to make better predictions about the future survival of insects and the animals that depend on them.

2.2 Materials and methods

2.2.1 Study site

The study was conducted at Tswalu Kalahari Reserve (27° 14' 55" S; 22° 22' 50" E), located in the semi-arid bioregion of the Northern Cape Province, South Africa. Tswalu covers ~114,000 hectares and consists of two sections: the Lekgaba and Korannaberg sections (Figure 2.1). The Korannaberg section is ~100,000 hectares in size and was the section of the reserve where the study was conducted. Air temperature ranged from −6 °C during winter to 42 °C during summer (onsite weather station, data by Vital Weather, powered by Davis Weather Instruments (Pty) Ltd; Hayward, 94545 USA) between 2014 and 2022. Weather at the site, which is within the summer rainfall area of southern Africa, is highly variable (Low and Rebelo, 1998; Tokura et al., 2018). Rainfall occurs mainly between December and February, with little or no rainfall from June to August (Dippenaar-Schoeman et al., 2018; Panaino et al., 2022).

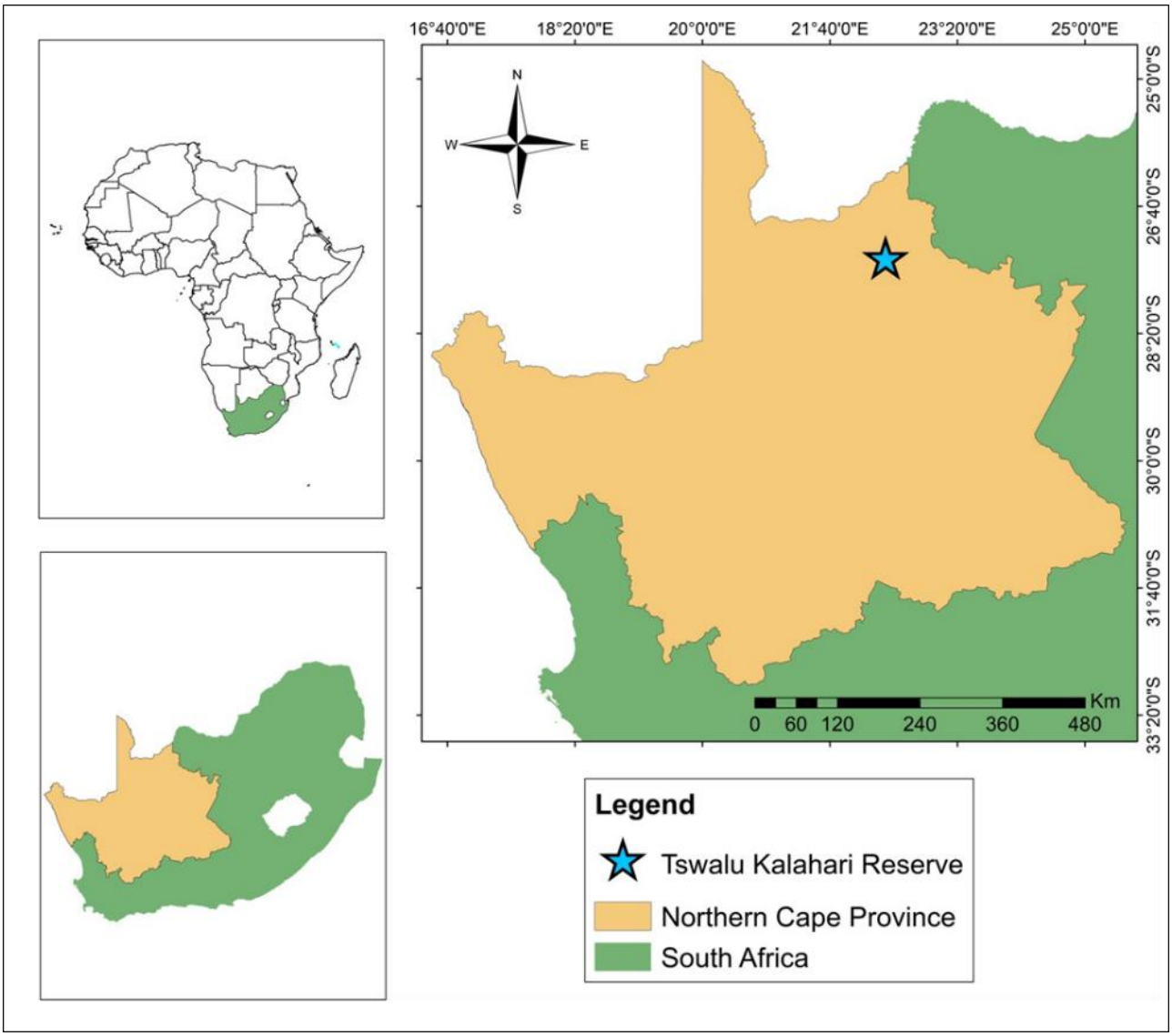

Figure 2.1: The study area at Tswalu Kalahari Reserve (right), located in South Africa (top left) within the Northern Cape Province (bottom left).

Tswalu has five major habitat types, namely the Kathu Bushveld, Olifantshoek Plains Thornveld, Gordonia Duneveld, Koranna – Langeberg Mountain Shrubveld, and Gordonia Plains Shrubveld (Tokura et al., 2018). Lions are absent from the Korannaberg section, although other carnivorous predators such as leopard, cheetah (*Acinonyx jubatus*), African wild dog, and spotted hyena roam freely. Mammals in the reserve that feed on insects include Temminck's pangolin, the aardvark, the aardwolf, and the bat- eared fox.

2.2.2 Air temperature and rainfall

Air temperature was recorded from the Tswalu Airstrip weather station (Vital weather) situated centrally at Tswalu. The daily rainfall was recorded from 33 rain gauges positioned across Tswalu, covering the area over which aardvark and pangolin were regularly observed.

2.2.3 Pitfall trapping of ants and termites

Pitfall trapping was conducted between September 2014 and August 2022. Between 20 to 40 transects were established across a variety of habitat types in which aardvarks and pangolins typically were found. Data collection started with 30 transects between September 2014 to October 2017. No data were collected between November 2017 and August 2018. Data collection resumed from November 2018 to August 2022 with sampling conducted every second month using 20 of the original transects, which were in the northern Tswalu section, an area associated with lower grass cover, and an additional 20 transects from the southern Tswalu area, with higher grass cover. The northern and southern areas differed in terms of grass cover because of differences in historical grazing pressure, with the northern area more heavily grazed historically.

The presence of ants and termites was assessed using pitfall traps (50 ml centrifuge tubes, conical bottom, 30 x 114 mm, BIOCOM Africa, South Africa). Each transect consisted of 10 pitfall traps, placed at 5 m intervals along a 50 m transect. The traps were placed in the ground, with the opening of the trap level with the ground surface for four days. Each trap contained 20 - 30 ml of a solution of antifreeze and water (100 ml antifreeze: 1 L water). The number of ants and termites that fell into each trap was counted; all other insects were excluded from the count and stored for future analyses. Based on previous research at the study site, the main prey items of Temminck's pangolin and the aardvark are *Crematogaster* and *Anoplolepis* ants, and *Trinervitermes* and *Hodotermes* termites; these prey items were identified and counted for further assessment. Ants and termites were identified to the genus level using the reference collections of ants and termites collected at Tswalu Kalahari Reserve by Dr Frederic Delsuc of the University of Montpellier and Dr Hamish Robertson of Iziko South African Museum, and a guidebook on the ants of southern Africa (Slingsby, 2017).The pitfall trap methodology that was used to assess ants

and termites was similar to that used in several previous studies (Swart et al., 1999; Pietersen, 2013; Weyer, 2018; Panaino et al., 2022, 2023).

2.2.4 Grass cover

Grass cover was estimated during the placement of pitfall traps, along each of the transects. At every 10 m along a 50 m transect, a basic vegetation survey was conducted using a 4 m^2 (2 x 2 m) plot, resulting in a total of 100 quadrats across the transects. To estimate the monthly average grass cover at each transect, the grass clumps within each 4 m^2 plot were counted. When a grass clump originated from a single stem, it was given a score of 1. When the base of a clump had between two and 10 shoots, it was given a score of 2, and when the base of a clump had more than 11 shoots, it was given a score of 3. The summed score of all clumps inside the quadrant was determined to estimate the average grass cover score. This method to estimate grass cover was adapted from Weyer (2018) and Panaino et al. (2022).

2.3 Data analysis

The data were summarized by month and season, where data existed, for air temperature, rainfall, grass cover score, and ants and termites in the traps. Seasons were classified as spring (September to November), summer (December to February), autumn (March to May), and winter (June to August). The air temperature was summarised as 24-h maximum, 24-h mean, and 24-h minimum (Appendix, Figure A1).

The ants and termites that fell into each of the pitfall traps from each transect were counted. The total number of ants and total number of termites were divided by the total number of pitfall traps retrieved (some traps were trampled on after deployment and were not excluded from the analysis), to estimate the average count of ants or termites per trap, every second month. From the pitfall traps, 17 ant and 6 termite genera were sampled.

Excel 2016, Graphpad Prism (version 8.0.2), and R (version 3.6.1 (RStudio: Intergrated Development for R studio, PBC, Boston, MA) were used to prepare raw data for statistical analysis and to generate graphs. Seasonal variation in prey abundance and grass cover were assessed using generalized linear models (with a negative binomial link) in R (package “lme4”) (Giraudoux, 2014; Kuznetsova et al., 2017), with season as a fixed effect

and transect number as a random effect. Where model effects were statistically significant, the estimated marginal means (R package “emmeans”) (Lenth and Lenth, 2017; Lenth et al., 2018) were used to identify statistically significant differences between seasons. Rainfall is known to positively affect grass cover and insect availability in the Kalahari (Weyer et al., 2020; Panaino et al., 2022), however, there may be a lag between rainfall and primary productivity (Dudney et al., 2017; van de Ven et al., 2020; Panaino et al., 2022).

To assess whether a lag predicted primary productivity better than the rain that fell during the same month as the transects were sampled, a lag of zero, one, two, or three months prior to each transect was analysed and Akaike information criterion (AIC) was used to assess the performance of each model. The model with the lowest AIC was then used in the generalized linear model to test the effects of rainfall on grass cover (Appendix, Tables A1 and A2). In instances where models had similar AIC values, a delta AIC value at least 2 lower than another model were considered superior (Burnham and Anderson, 2004). The data were first checked for normality using residual plots and Shapiro-Wilk tests in R. Results are reported as mean ± SD.

2.4 Results

2.4.1 Air temperature

The mean monthly air temperature at Tswalu between September 2015 and August 2022 varied from an absolute daily minimum winter air temperature of −5.1 °C to a maximum daily summer air temperature of 42.0 °C. Average monthly temperatures typically varied between 10 and 30 °C (Figure 2.2). In 2015 there was only one month of data, over spring, that was recorded. Between 2015 and 2022, the summer of 2019 was the warmest with mean air temperature of 29 °C and mean maximum air temperature of 37 °C. Between 2015 and 2022, the winter of 2020 was the coldest with a mean air temperature of 13 °C and a mean minimum air temperature of 5 °C (Figure 2.2; Figure 2.3; Appendix Figure A1).

2.4.2 Rainfall

The average annual rainfall between September 2015 and August 2022 was 282 mm (Figure 2.2). From mid-2020 to mid-2021, rainfall was 517 mm, and this period was the

wettest period during the study. It was also the period with the highest annual rainfall received at Tswalu since 2001. The year 2021 also received the highest rainfall (206 mm) in January. Between 2017 and 2020, rainfall generally declined and was 107 mm in 2019, until it increased in 2021 (Figures 2.2 and 2.3; Appendix Figure A1).

2.4.3 Grass cover

Grass cover score varied across the study years between 2015 and 2022. The annual grass cover score was lowest (9) on average in 2019 and highest (42) in 2022 (Figure 2.2; Figure 2.3; Appendix Figure A1). The grass cover score was low (< 20) in the first two years of the study period (2015 and 2016), then reached a high score during the summer of 2017 (26). Between 2017 and 2018, grass cover decreased and only showed an increase (> 30) again during summer of 2021 and 2022.

The grass cover score was at its highest (47) during summer at the beginning of 2022 following the high rainfall that occurred in 2021. The grass cover score was also high (> 40) during autumn and winter of 2022 and was low (< 35) during spring of 2022. AIC modelling showed that the effects of accumulated rainfall three months prior to the assessment of the transects produced the best model for grass cover analysis compared to rainfall that fell during the months when transects were assessed or accumulated rainfall that fell four, two, and one month prior to the assessment of the transects (Appendix Tables A1 and A2). Rainfall three months prior was thus used in the linear mixed model. When the accumulated rainfall in the preceding three months was high, and when environmental temperature was high, grass cover was high.

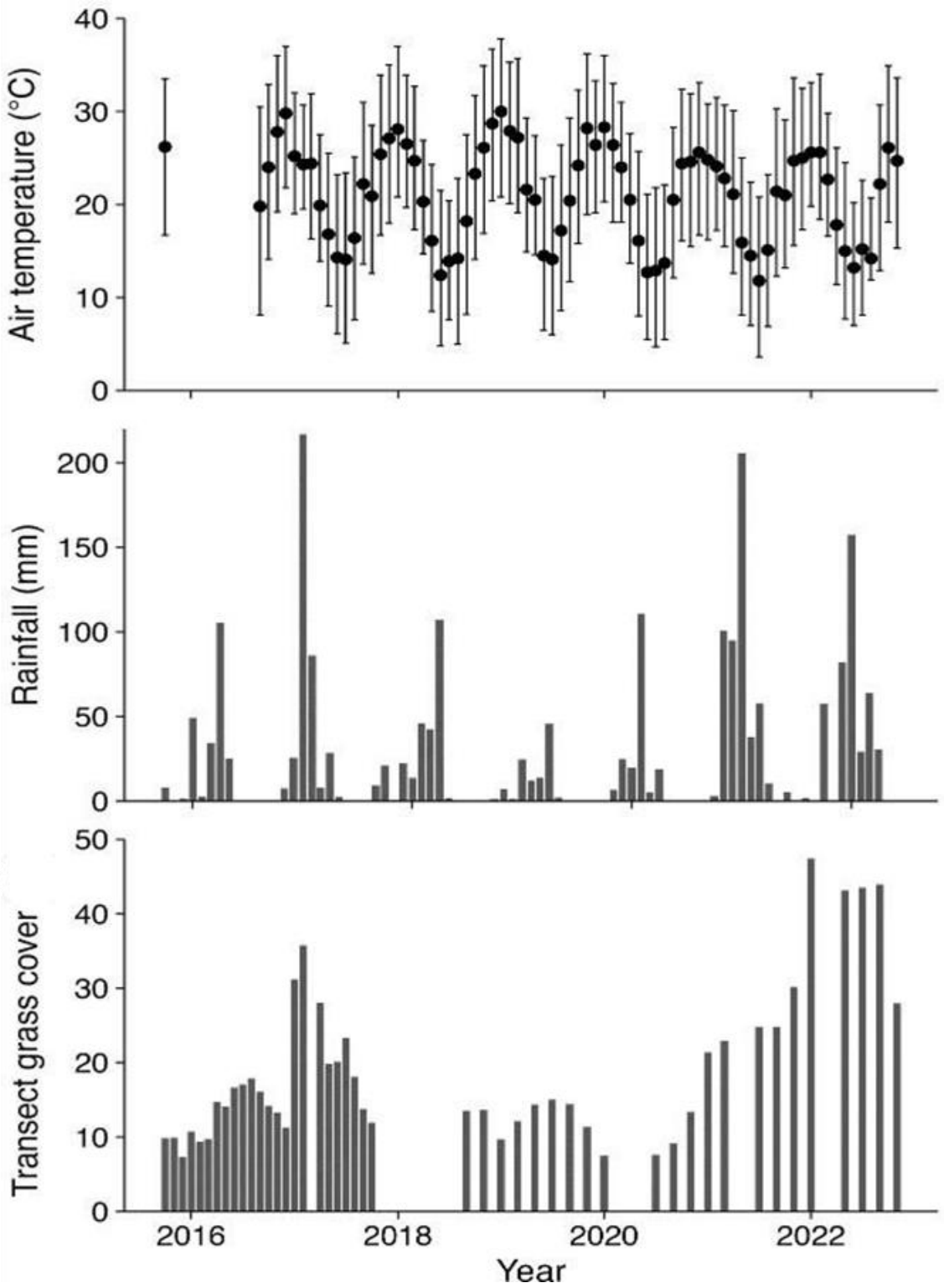

Figure 2.2: Monthly records of air temperature, rainfall and grass cover at Tswalu Kalahari Reserve, Northern Cape province, South Africa between September 2015 and November 2022. In 2015, only one month of the spring data were recorded.

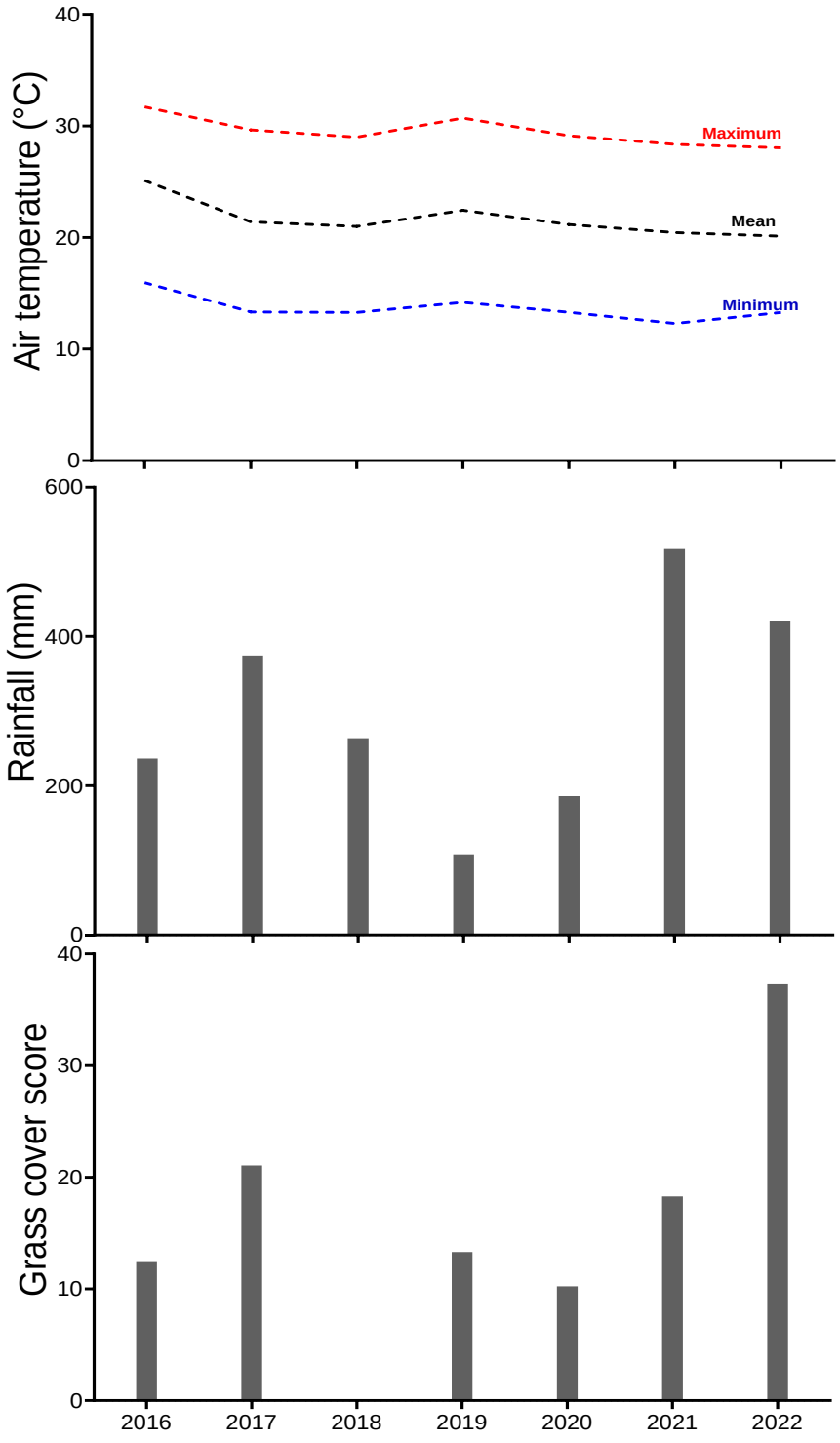

Figure 2.3: Mean annual records of air temperature, rainfall and grass cover at Tswalu Kalahari Reserve, Northern Cape province, South Africa between September 2015 and November 2022.

2.4.4 Ants

The average number of *Anoplolepis* ants per trap increased during the initial period of the study between 2015 and 2016 reaching a high of 150 ants per trap in 2016, and then declined, until the ants per trap increased again between 2021 and 2022 (Figures 2.4 and 2.5). During summer of 2022, the average number of *Anoplolepis* ants in the traps was high (~244 ± 338 ants per trap) and during summer of 2022 it was low (~10 ± 40 ants per trap). The average number of *Anoplolepis* ants was higher (~141 ± 346 ants per trap) during autumn of 2021 than during autumn seasons of the other study years. The average number of *Anoplolepis* ants was lower (~4 ± 14 ants per trap) during winter periods than during the other study seasons (Figure 2.4; Figure 2.5; Appendix Figure A2). The linear mixed model revealed that the number of *Anoplolepis* ants per trap was positively associated with minimum air temperature and grass cover (β = 1.18, SE = 0.0088, t = 21.73, P < 0.001) and grass cover (β = 1.06, SE = 0.0023, t = 27.20, P < 0.001). When minimum air temperature and grass cover increased the average number of ants per trap increased (Appendix Tables A3 and A4).

The average number of *Crematogaster* ants per trap showed an overall decreasing trend across the study years (Figures 2.4 and 2.5). The average number of *Crematogaster* ants per trap was low (< 6 ants per trap) from September 2015 until it increased (16 ants per trap) in May 2019. The average number of *Crematogaster* ants per trap decreased (2 ants per trap) drastically from June 2019, increased (10 ants per trap) in July 2021 and decreased again in the remaining study months. The average number of *Crematogaster* ants per trap was high (~10 ± 63 ants per trap) during winter of 2021 and low (~1 ± 9 ants per trap) during winter in the other study years. *Crematogaster* ants per trap were high (8 ± 48 ants per trap) during autumn of 2019 and did not occur in pitfall traps during autumn of 2020 (Figures 2.4 and 2.5; Appendix Figure A2). The linear mixed model revealed that the number of *Crematogaster* ants per trap was negatively associated with maximum air temperature (β = 0.90, SE = 0.03, t = -2.87, P = 0.004) and grass cover (β = 0.95, SE = 0.02, t = -2.37, P = 0.018), but not significantly associated with rainfall (β = 0.98, SE = 0.01, t = -1.42, P = 0.155). *Crematogaster* ants were less likely to be found in areas with higher temperatures or more extensive grass cover, than *Anoplolepis* ants (Appendix Tables A5 and A6).

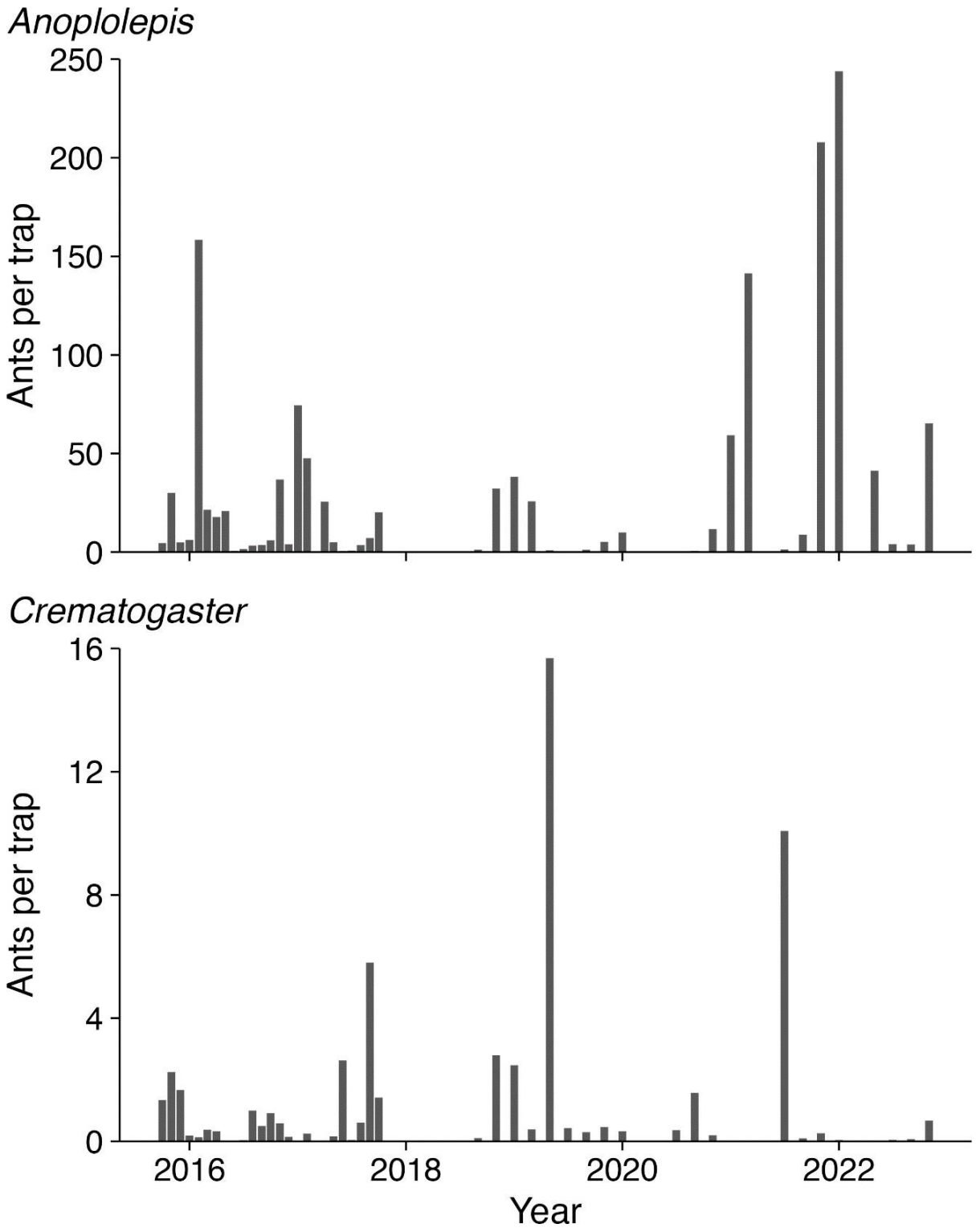

Figure 2.4: Mean ants (*Anoplolepis* and *Crematogaster*) per trap during transect assessment months at Tswalu Kalahari Reserve, Northern Cape province, South Africa between September 2015 and August 2022.

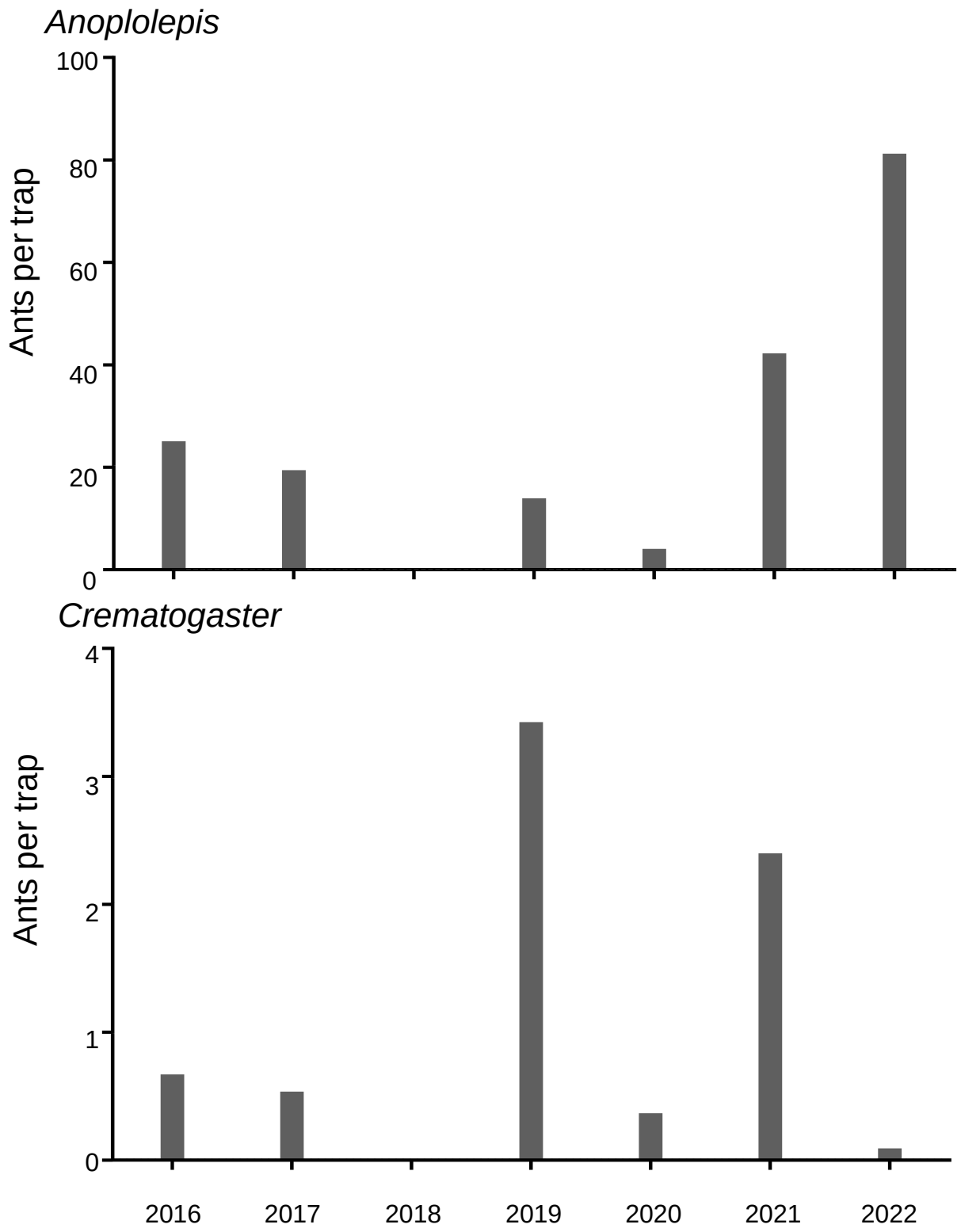

Figure 2.5: Mean ants (*Anoplolepis* and *Crematogaster*) per trap during transect assessment at Tswalu Kalahari Reserve, Northern Cape province, South Africa between September 2015 and August 2022.

2.4.5 Termites

The average number of *Hodotermes* termites per trap showed a decreasing trend during the study period (Figures 2.6 and 2.7). The average number of *Hodotermes* termites in the traps' during spring of 2015 was 4 ± 21 termites per trap. The average number of *Hodotermes* termites per trap increased (7 termites per trap) in January 2016 and decreased again (4 termites per trap) in April 2016. The average number of *Hodotermes* termites per trap increased (5 termites per trap) in September 2016 and reached a peak (8 termites per trap) in October 2016. The average number of *Hodotermes* termites per trap continued to decrease and was lower (5 termites per trap) during the rest of the study period (Figures 2.6 and 2.7; Appendix Figure A3). From 2019 to 2022, *Hodotermes* termites did not occur in the pitfall traps during winter (Figures 2.6 and 2.7; Appendix Figure A3). The linear mixed model revealed that the number of *Hodotermes* termites per trap had no positive association with grass cover (β = 0.92, SE = 0.03, t = -2.88, P = 0.004), but not significantly associated with maximum air temperature (β = 1.03, SE = 0.04, t = 0.73, P = 0.468) (Appendix Tables A7 and A8).

The average number of *Trinervitermes* termites per trap also showed a decreasing trend during the study period (Figures 2.6 and 2.7). The average number of *Trinervitermes* termites per trap was highest (5 termites per trap) in November 2015 and was lower (2 termites per trap) in December 2015 and January 2016. The average number of *Trinervitermes* termites per trap increased (15 termites per trap) in February 2016 and decreased (< 3 termites per trap) during the rest of the study years (Figures 2.6 and 2.7). The average number of *Trinervitermes* termites in the traps was high (6 ± 14 termites per trap) during summer of 2016 and was low (below 2 termites per trap) during the rest of the summers of the study period (Figures 2.6 and 2.7; Appendix Figure A3). During the winter of 2020 and 2021, *Trinervitermes* termites did not occur in all the pitfall traps (Figure 2.6; Appendix Figure A2). The linear mixed model revealed that the number of *Trinervitermes* termites per trap was not significantly associated with maximum air temperature (β = 1.09, SE = 0.12, t = 0.79, P = 0.429) or grass cover (β = 0.85, SE = 0.10, t = -1.36, P = 0.175) (Appendix Tables A9 and 10).

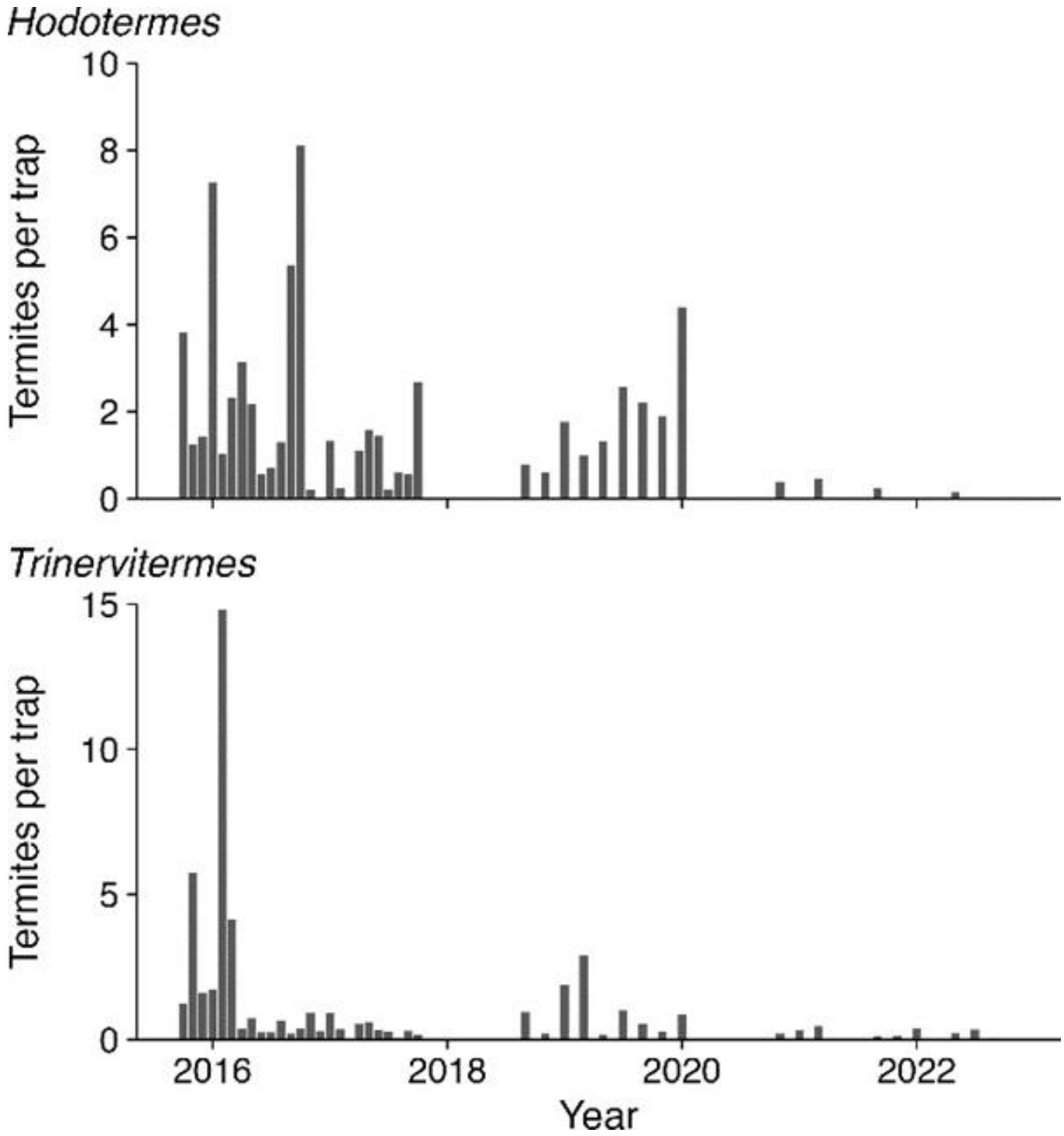

Figure 2.6: Mean termites (*Hodotermes* and *Trinervitermes*) per trap during transect assessment months at Tswalu Kalahari Reserve, Northern Cape province, South Africa between September 2015 and August 2022.

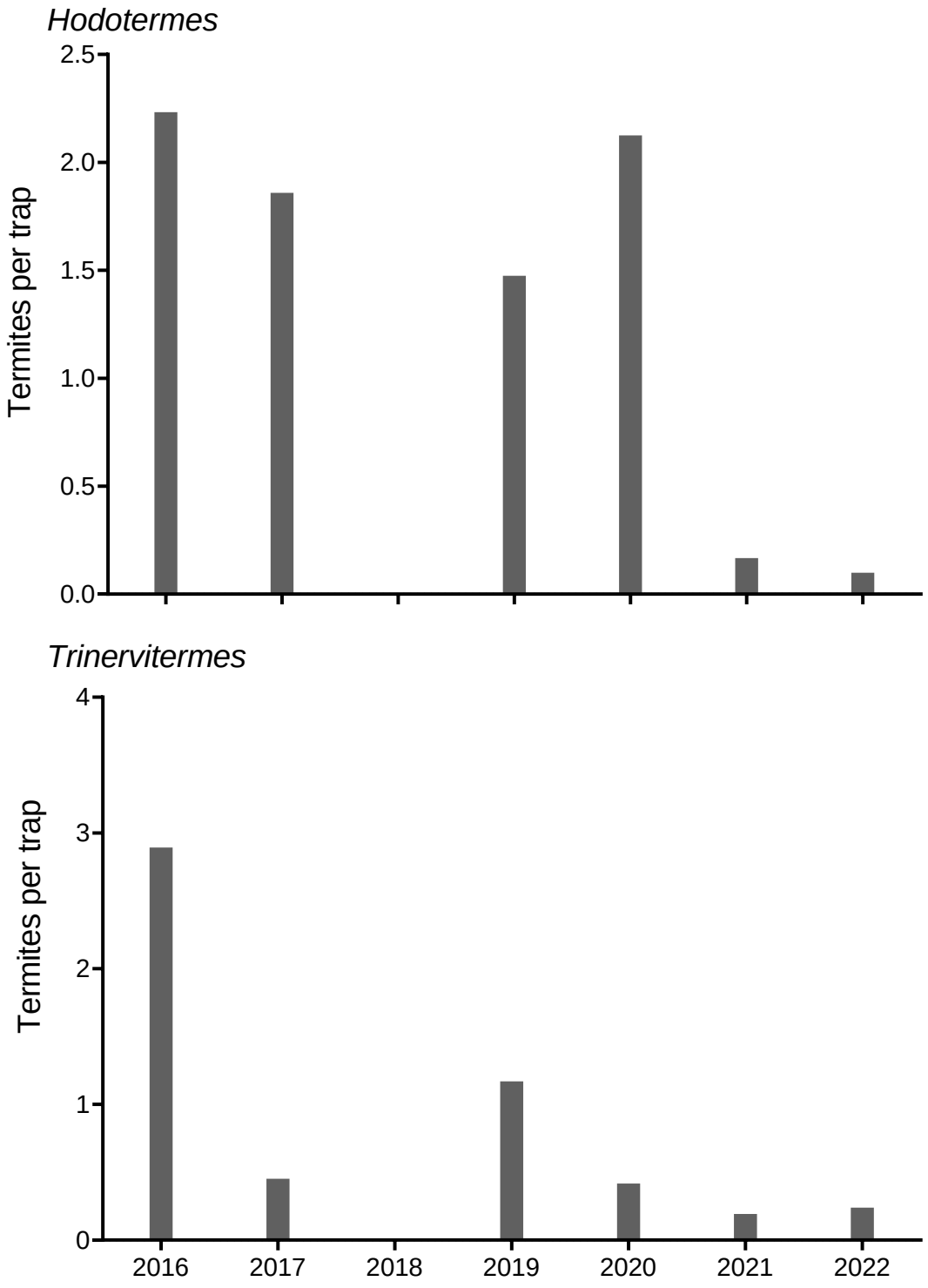

Figure 2.7: Mean annual termites (*Hodotermes* and *Trinervitermes*) per trap assessment at Tswalu Kalahari Reserve, Northern Cape province, South Africa between September 2015 and August 2022.

The 8-year data (2014 and 2022) collected at the study area are shown in Figure 2.8. The data reveal a general decreasing trend for ants and termites in pitfall traps, but an increase in ant numbers in pitfall traps following rainfall between 2020 and 2021. In contrast, termite numbers continued to decrease even after the rainfall of 2020 and 2021 (Figure 2.8).

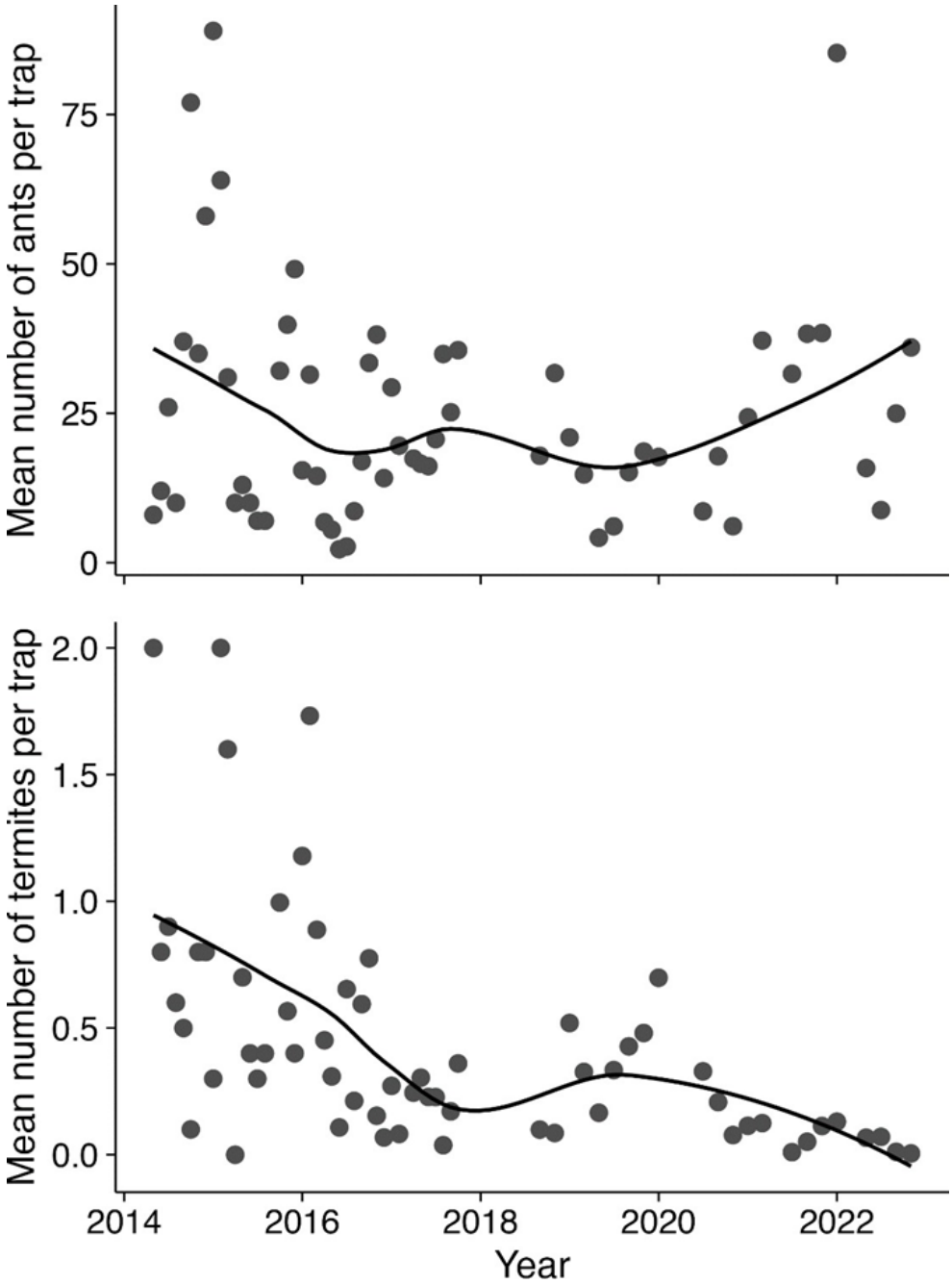

Figure 2.8: Mean monthly number of ants and termites per trap for the period between 2014 and 2022, showing seasonal fluctuations (black dots) and the overall decreasing trend (black solid line) at Tswalu Kalahari Reserve, Northern Cape province, South Africa.

2.5 Discussion

I assessed how patterns of grass cover, as well as the number of ants and termites in pitfall traps, varied over the eight-year (2014 – 2022) study period in Tswalu Kalahari Reserve. From 2014 to 2019, the number of ants and termites in traps generally decreased. In my dataset, the year 2019 was the hottest and driest year, and was accompanied by relatively low grass productivity. In association with the La Niña event between 2020 and 2022 (Mpungose et al., 2022; Geng et al., 2023), rainfall increased, particularly between 2021 and 2022. The period was followed by an increase in grass cover and in the number of ants in pitfall traps. In contrast, termite numbers continued to decrease even after the high rainfall. Of the four main prey items known to be preyed on by Temminck's pangolin and aardvark in Tswalu Kalahari Reserve, *Anoplolepis* ants and *Trinervitermes* termites appeared to be the most affected by the heat and aridity, as shown by the low trap counts in 2019. Counts of both *Trinervitermes* and *Hodotermes* termites in the traps were lowest after 2020, despite the high rainfall and higher grass cover.

One limitation in drawing conclusions on the availability of ants and termites over time is the use of pitfall traps, which may underestimate the availability of arboreal and subterranean species. The actual availability of arboreal (*Crematogaster*) or subterranean (*Hodotermes, Trinervitermes, Anoplolepis*) ants and termites may therefore have been much higher than observed in the traps (Jones et al., 2005). By ceasing surface activity when it is hot and dry, ants and termites would be less likely to fall into the pitfall traps but may still have been available to the pangolins and aardvarks in their arboreal or subterranean nests (Davies et al., 2015; Panaino, 2021). On the other hand, termites tend not to move too far to forage when food (grass) is near and hence may have been less likely to fall into the traps when grass cover was high (Ahmad et al., 2018; Korb, 2021). Pitfall trapping likely reflects a count influenced by both abundance and levels of activity. There may be instances where the termites are in abundance but there is little surface activity and thus their presence is not recorded. Nevertheless, the pitfall traps reflected expected seasonal patterns of insect availability, with higher trap counts (even for termites, despite the low absolute counts) during summer than during winter, so the long-term use of pitfall traps may serve as a simple but valuable tool for assessing changing trends in insect abundance in response to changes in environmental conditions. In addition, there

are other methods that can be used to assess termites other than direct observation and trapping techniques, including soil sampling, DNA analysis, and behavioural studies. These methods should be employed in future studies to confirm the effects of climate change on termite populations.

During periods of low rainfall in the study area, the scarcity of grass cover would have resulted in a reduction of available food resources (grasses) that are available to ants and termites. Grasses serve as a primary source of food for ants and termites, providing essential nutrients and energy. When rainfall is insufficient, the growth of grass slows, leading to reduced grass cover. Low rainfall hinders nest construction and tunnelling activity (Deeming and Campion, 2018; Standish et al., 2018; Rojas et al., 2019), as insects may conserve energy and resources during water scarcity, resulting in reduced trap captures. The decline in rainfall between 2017 and 2020 during the study likely contributed to the decline in grass cover during that period. In addition, the average grass cover score that was recorded in 2020 was only one third of grass cover score that was recorded in 2022 following heavy rainfall.

Lower grass likely led to lower ant and termite numbers. Grasses influence soil moisture and microclimate, impacting ant and termite nesting (English et al., 2005; Véle and Holuša, 2008; Trisos et al., 2021). A reduction in grass cover is likely to create less favourable nesting conditions, affecting the overall suitability of the habitat for ants and termites. The impact of low grass cover on the availability of ants and termites reported in this study is similar to that previously reported by Weyer (2018) and Panaino (2021). As the Kalahari is a semi-arid environment with conditions of low rainfall and high temperatures (Parmesan et al., 2000; Holmgren et al., 2006), these climatic conditions will inevitably impact the availability of food resources for species. The species richness of ants and termites is generally higher on botanically diverse grasslands (Kruess and Tscharntke, 2002). Thus, low grass cover will lead to fewer ants and termites with consequences for the animals that prey on the ants and termites.

Ant and termite populations are a key prey resource for many myrmecophagous mammals, including the aardvark and pangolin (Redford, 1987, Pietersen et al., 2014; Weyer et al.,

2020). In the absence of these prey items, specialist myrmecophagous mammals will starve to death. Previous research at the study site has shown that four main prey items are known to be preyed on by pangolin and aardvark, namely *Crematogaster* and *Anoplolepis* ants, and *Trinervitermes* and *Hodotermes* termites. Following a severe drought in the study area between 2013 and 2017, associated with low numbers of ants and termites, five of the aardvark individuals that were part of a study at Tswalu, as well as 11 other aardvark individuals at the study site, were found dead in poor body condition reflecting starvation (Rey et al., 2017; Weyer et al., 2020). In 2019, a very hot and dry year in which pangolins were tagged for study, five of the pangolins experienced starvation and died. Following the summer of 2021, the study area experienced above average rainfall and the vegetation productivity across the study site recovered, with no deaths reported for pangolins, which were still being tagged and closely studied. While aardvarks at the study site were not being closely monitored, there also were no reports of death for this species.

Changing rainfall patterns or shifts in the timing of rainfall are often associated with alterations in vegetation growth and distribution. These changes can have profound effects on ecosystems, impacting food resources and overall productivity. Although the Kalahari is a dryland, it experienced heavy rainfall from the La Niña events that occurred between 2020 and 2021, resulting in increased grass cover (Olivier et al., 2020; Li et al., 2022). The increase of grass cover seen during autumn and winter of 2021 was likely from rainfall during the previous months (Dudney et al., 2017), with rainfall occurrence in the preceding summer, and some rainfall extending into March 2022. When compared to previous years in the Kalahari, my study site experienced the highest rainfall recorded since 2001.

Following the high rainfall that occurred, the availability of ants and termites increased (Dangerfield, 1998; Ridley and Raihani, 2007). Ants and termites, however, responded differently to the high rainfall and the growth of grass cover associated with the La Niña event between 2020 and 2021. Ants are opportunistic foragers, and more rainfall provides diverse food resources for them, while less rainfall may reduce ant richness (Davidson, 1977; Fourcassié and Oliveira, 2002; de Almeida et al., 2020; Sundaram et al., 2022). Ant species also build their nests in soil, and following a rainfall event, the soil is soft and can

facilitate the construction or expansion of ant nests (Li et al., 2014; Luke et al., 2014; Lamb et al., 2020). Higher grass cover can also provide suitable nesting sites, resulting in a positive response in ant populations (Heller et al., 2008; Luke et al., 2014; Lamb et al., 2020). In addition, ants are known for their adaptability, and different species may exploit various niches within the changing environment (de Bruyn and Conacher, 1990). The growth of grass cover may benefit termites that primarily feed on dead plant material, providing an abundant food source, as some species specialize in decomposing dead plant material (Brauman, 2000; Holt and Lepage, 2000; Ibrahim and Adebote, 2012). Increased rainfall can also facilitate nest construction and maintenance, particularly for termite species that construct extensive underground tunnels (Wood, 1988; Buxton, 2004; Abe et al., 2009; Bonachela et al., 2015).

Despite the possible benefits of increased rainfall, only the ant numbers in the traps increased following the high rainfall between 2020 and 2021. The decrease in the number of termites might be associated with a decrease in the populations of termites in the area, or perhaps might reflect termites going deeper underground. The nests of *Hodotermes mossambicus* are subterranean, and up to 6.8 m (usually 1 - 1.5 m) underground, where they are believed to form ideal refuges from environmental extremes (Mitchel et al., 1993). Termites have specific developmental stages that can be sensitive to environmental change, while ants appear to be less sensitive across developmental stages (Korb and Hartfelder, 2008; Woon et al., 2022). Termites move slowly because of their physiology and behaviour, as well as their preferred habitat (Reinhard and Kaib, 2001; Olugbemi, 2010). Slower movement in individual termites also may be due to frequent stops and turns, and a strategy to escape danger in an exposed area (Xiong et al., 2018). Termites are also known to build underground nests that can withstand flooding, and they withdraw during intense rain to protect their colonies (Jones, 2003). In contrast, ants in arid regions, such as the Kalahari, often forage after rain, as moisture enhances food availability leading to an increase in surface activity and making ants easily accessible on the ground (Pietersen, 2013; Weyer, 2018; Panaino et al., 2022). In addition, rain can aerate porous ant nests, providing benefits such as moisture regulation, improved oxygen levels, temperature control and nutrient transport (Culliney, 2013; Li et al., 2014; Farji-Brener and

Werenkraut, 2017). These factors collectively maintain optimal colony conditions and support ant colony health (Culliney, 2013).

In my study, the number of *Hodotermes* termites in the traps was not associated with maximum air temperature but was negatively associated with grass cover. When there is more food (grass) around, termites probably do not have to move far to forage, and hence may be less likely to fall into traps. It is also possible in my study that termite populations decreased after the rain, but studies conducted elsewhere indicate that termite numbers increase following rainfall (Vohland and Deckert, 2005; Lind et al., 2022). Many ant and termite species, including the ones at the study site in the present study have specific periods during which they engage in mating and dispersing to establish new colonies (Korb and Schmidinger, 2004; Chouvenc, 2022). If the timing of rainfall shifts due to changing weather patterns, it could disrupt these mating flights and colony establishment, potentially leading to population declines (Parr and Bishop, 2022). Rainfall can impact the ability of insects to forage, finding nesting sites, and maintaining colonies (Belchior et al., 2012; Fisher et al., 2021; Yang et al., 2021).

High temperatures can directly affect ants and termites through impacts on their metabolic rates, activity levels, and water use in arid conditions (Ahmed et al., 2011; Parr and Bishop, 2022). Arid conditions may limit the availability of resources such as food, water, and suitable nesting materials, which can in turn affect the population dynamics. Extremes in the maximum daily air temperature can directly impact ants and termites, resulting in mortality. In the last few decades, there has been an increase in temperature extremes and heat waves in South Africa (Ncongwane et al., 2021; Mbokodo et al., 2023). Insects have a thermal maximum that is relatively consistent among all species and if exceeded will cause mortality from a loss of motor control (Addo-Bediako et al., 2000; Sunday et al., 2011). Insects present in hot ecosystems, such as those in the Kalahari, are thus predicted to be the most impacted by extreme heat events in the future (Weyer, 2018). Recent studies indicate that hot extremes can also negatively affect temperate species such as processionary moths (Rocha et al., 2017) and bumble bees (Oyen et al., 2016). In addition to exceeding thermal maxima, extreme heat negatively affects insect behaviour and development (Hamblin et al., 2017; Harvey et al., 2020).

The heat and aridity in some years in my study area appeared to impact the population numbers of *Anoplolepis* ants. Ants are sensitive to high environmental temperatures (Porter and Tschinkel, 1993). The foraging activity of *Anoplolepis* ant is affected by ambient temperature, with the highest activity levels between 26 °C and 30 °C (Chong and Lee, 2009). *Anoplolepis* ants in the pitfall traps decreased during the hotter periods of my study and only increased after the summer rainfall. In addition, I found that the number of *Anoplolepis* ants in traps was positively associated with minimum air temperature and grass cover. By the end of the dry period with low grass cover, the *Anoplolepis* ants count was at an all-time low, but soon after rain, the numbers rapidly increased, as shown by an increased number in the pitfall traps. The *Anoplolepis* ant is also known to increase surface activity following rainfall (Swart et al., 1999). As seed harvesters (Witt and Giliomee, 2005), they likely cease foraging activity and remain underground until rainfall events because of the absence of grass seed production during the dry months, making the ants less likely to fall into the pitfall traps.

Extreme air temperatures and low grass cover may pose challenges to the survival of termites, specifically *Hodotermes* and *Trinervitermes* termites, because their presence is dependent on the availability of dietary plant material, typically dry grass (Nel and Hewitt, 1969). *Hodotermes mossambicus* harvests dry grass during autumn and winter (Mitchell et al., 1993). *Hodotermes mossambicus* workers have been observed to cut fresh and dead grass, transport the grass, and make grass storage areas around foraging ports (Duncan and Hewitt, 2009; Picker et al., 2019). When the diet of the *H. mossambicus* was investigated at two sites with distinct dietary components, it was found that grass represented approximately 93% of its diet (Symes and Woodborne, 2011). *Trinervitermes* termites forage on grass at night. During the day, foragers withdraw to the nest and make granaries in de-vegetated areas (Adam et al., 2012; Picker et al., 2019). *Trinervitermes* termites are known as grass litter feeding termites capable of harvesting approximately 20% of the standing grass biomass during normal seasons (Coaton, 1951), and during drought the harvest can reach 60% (Hartwig, 1955).

Assessing long-term patterns of grass cover and the populations of ants and termites in an environment is crucial for understanding how they may impact the ecosystem over time

(Tokura et al., 2018), and particularly, in response to the stressors arising from climate change. Grasses, ants, and termites are key components of the Kalahari ecosystem. Changes in their numbers in the ecosystem are likely to serve as indicators of broader ecological shifts. Ant and termite availability generally decreases in the absence of rainfall. Although ant populations appear to have recovered following high rainfall in the study, it is less certain if the same is the case with termite populations. Indeed, the overall trend in my data is a decline in the numbers of ants and termites. If the study area experiences an increased frequency or longer duration of droughts in future, insect availability may again decrease substantially, resulting in the starvation and death of myrmecophagous animals in the area. Exploring the long-term influence of climate on vegetation also will allow for a better understanding of how these insects will likely respond in future. Thus, it is crucial to continue with this type of long-term monitoring to have better predictions for the future of insect populations in drylands. The findings of this study provide invaluable insights into the potential consequences of climate change, and the need for well-informed decisions that underpin the evaluation and management of the Kalahari ecosystem

Chapter 3 - Dietary overlap between the aardvark and ground pangolin in the Kalahari

3.1 Introduction

At least 216 mammal species feed on ants and termites, and of these, about 12% are myrmecophagous species (Redford, 1987). The aardvark and Temminck's pangolin are nocturnal myrmecophagous mammals that have several adaptations that facilitate their specialisation feeding on ants and termites (Willis et al., 1992; Taylor et al., 2002; Pietersen et al., 2016b). In southern Africa, the aardvark has been shown to feed primarily on termites, but ants can constitute an important part of its diet (Willis et al., 1992; Lindsey, 1999; Pietersen and Robertson, 2023), whereas the pangolin generally prefers ants but will also consume termites (Richer et al., 1997; Pietersen et al., 2016b; Prediger, 2020).

Species with similar ecology, like the aardvark and pangolin, can exist sympatrically because of niche partitioning, which can reduce competition for resources (ter Schure et al., 2021; Pietersen and Robertson, 2023). The apparent dietary niche separation between the aardvark and pangolin suggests that little competition likely occurs between these species. Although the diet of the aardvark and pangolin has been compared through a literature survey of data from different studies and regions (Pietersen and Robertson, 2023), no study has assessed the diet of the two species simultaneously in the same environment. Understanding dietary preferences and dietary overlap, along with how the diet may change with environmental impacts on the availability of prey species, is a key aspect in determining the presence and persistence of these mammals (Correa and Winemiller, 2014). Such knowledge is also crucial for developing conservation plans for the aardvark and pangolin, in terms of habitats that need to be conserved, and understanding their impacts on the ecosystem (Redford, 1987; Challender, 2009).

The semi-arid Kalahari of southern Africa, a region in which aardvarks and pangolins co-exist, is likely to become hotter and drier with climate change (Rey et al., 2017; Weyer et al., 2020; Panaino et al., 2023), potentially with negative impacts on the abundance of their insect prey (Weyer et al., 2020). Declining insect prey abundance could have significant implications for the survival of certain species (Maurice et al., 2019; Juillard and Ramp, 2022). The aardvark and pangolin may be particularly vulnerable to sustained declines in insect prey abundance if they may compete for the same food resources (Craigie et al., 2010; Kiffner et al., 2017). Previous research conducted in the Kalahari showed that a

decline in ant and termite populations (as indicated by counts in pitfall traps) associated with drought resulted in starvation of aardvarks and pangolins (Weyer et al., 2020; Panaino et al., 2022). The diet of these two mammals in the Kalahari does not appear to overlap much, with aardvarks shown to prey predominantly on harvester termites (*H. mossambicus*) (Weyer et al., 2020) and pangolins preying predominantly on ants (mainly *Crematogaster* ants.) (Panaino et al., 2022). However, the research on the diet of the two species was conducted at different times, so the dietary differences may have arisen from various factors that differed between the study periods, including a difference in prey species abundance (Pietersen and Robertson, 2023).

I therefore determined the diet of aardvarks and pangolins in the same environment at the same time via the collection of faecal samples in the Kalahari over one year, to assess possible dietary overlap. I measured grass cover, as the ants and termites rely on grass for food and habitat (Geerts et al., 2016; Kasseney et al., 2019). I related the diet and dietary overlap of the two mammal species to the abundance of prey items, as assessed by pitfall trapping. I hypothesized that aardvarks would show a preference towards termites in their diet, while pangolins would prefer ants, and that the diets of both mammals would not simply reflect the most abundant prey items.

3.2 Materials and methods

3.2.1 Study area

The study was conducted in the same area as explained in section 2.2.1 in Chapter 2. The data for this chapter were collected between September 2020 and August 2021.

3.2.2 Pangolin tracking

Prior to the start of the study, four (3 female and 1 male) adult pangolins (5.9 – 9.6 kg) were captured opportunistically and fitted with tracking transmitters. A Very High Frequency tracking transmitter (~40 g; 55 x 32 mm) (custom-made, Africa Wildlife Tracking, Pretoria, South Africa) was attached to a dorsolateral scale of each animal using a 3 mm bolt fixed through a hole drilled into a non-vascular portion of a scale. The transmitter was attached in about 10 minutes without the use of anaesthetic drugs, as done in other studies on pangolin (Pietersen et al., 2014a; Meyer et al., 2020; Panaino et al.,

2022). After the tracking transmitter was secured to the scale of the pangolin, the animal was released.

3.2.3 Prey abundance

Prey abundance was assessed using pitfall traps, following the methodology outlined in section 2.2.3 in Chapter 2. However, for this chapter, a modified approach was adopted, where 20 transects were placed every second month over one year period, from September 2020 to August 2021.

3.2.4 Air temperature and rainfall

Air temperature data were recorded from airstrip weather station (Vital weather) located at Tswalu Kalahari Reserve. Daily rainfall data were recorded from 33 rain gauges positioned across the reserve covering the entire area that the aardvark and pangolin used. The data collection method was as described in section 2.2.2 in Chapter 2, with the only difference being that the study year for this chapter was from September 2020 to August 2021.

3.2.5 Grass cover

Grass cover score was similarly recorded as explained in section 2.2.4 in Chapter 2.

3.2.6 Faecal collection

3.2.6.1 Aardvark faecal samples

Aardvarks were not tagged with tracking transmitters for the purposes of this study, but scats were located opportunistically by searching for signs of aardvark activity, such as fresh tracks, followed the tracks until a relatively fresh scat was located. It was much easier to locate aardvark faeces without following an animal than it was for a pangolin. An aardvark deposits its scat in a shallow furrow which it then covers up, leaving behind a distinctly shaped mound that is completely covered with soil, and often a tail indent is present above the mound (Figure 3.1). I dug out the scats from the hole which are oval containing termites or ants and soil particles which they cannot help but digest when they dig for prey items (Figure 3.2).

Figure 3.1: An aardvark (*Orycteropus afer*) defaecation (scats) site covered with sand/soil making a distinctly shaped mound, leaving behind a tail sign impression on top of the soil, at Tswalu Kalahari Reserve in the Northern Cape province of South Africa.

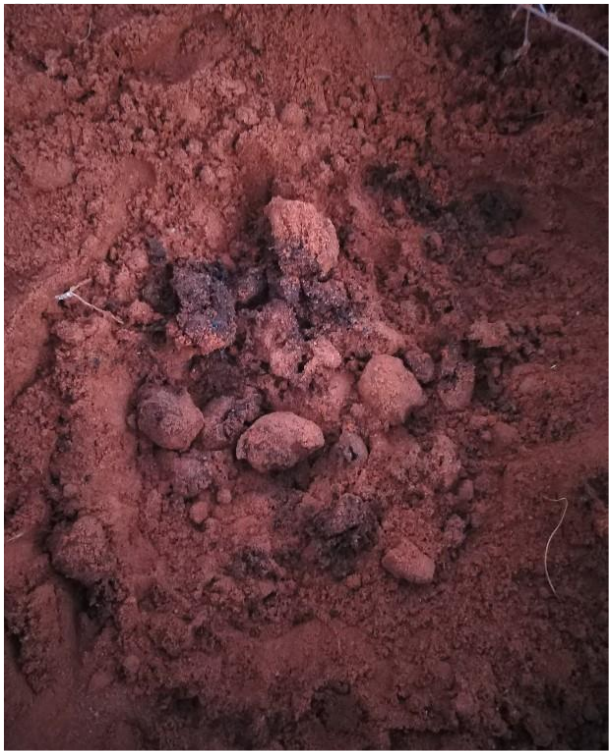

Figure 3.2: Aardvark (*Orycteropus afer*) scats are oval, with about 15 to 50 oval-shaped pellets containing chitinous remains of the insect prey covered by soil particles. The pellets are brown to dark brown in colour.

I used a GPS device to accurately record the coordinates of each scat location to ascertain that scats were not likely collected more than once from the same individual on a given day (Figure 3.3). Two outlier locations were excluded because they were more than 11 km away from a polygon surrounding the other locations. I then calculated the area across which the scats were collected and related that area to the reported home range of aardvark in the Karoo (between 1.3 and 3.5 km^2; Taylor and Skinner, 2003). I collected scats over an area of 15 km^2, thus, it is likely that I collected scats from between 5 and 12 individual aardvarks. The number of faecal samples collected varied between 1 and 30 per month, with a total of 93 faecal samples collected in total (Table 3.1). I collected only fresh faecal samples, as indicated by the softness and wetness of the sample. The faecal samples were stored in resealable plastic packets (Glad Products Company, California, USA) for later analysis.

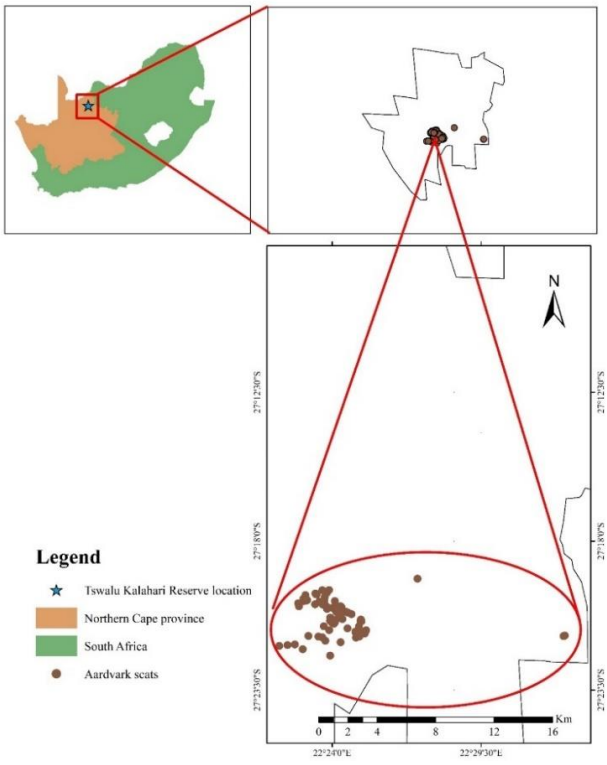

Figure 3.3: The distribution of aardvark (*Orycteropus afer*) scat locations within the Duneveld area of Tswalu Kalahari Reserve, Northern Cape province, South Africa. Each marked point represents a site where aardvark scat was found, indicating the animal's habitat use and movement patterns within the reserve.

3.2.6.2 Pangolin faecal samples

The four tagged pangolins were followed during their active phase at a sufficient distance to prevent disturbing them, until they defaecated. Once the animal moved away from its fresh scat, the scat was collected. There was a characteristic behaviour associated with defecation by the pangolin; it would pause, spread its hind legs, dig a small hole using its front legs, and then defaecate sausage-shaped scats into the hole (Figure 3.4). The number of samples collected each month varied between 1 and 4 from different individuals. The collection of pangolin scats was particularly difficult because they often defaecate deep inside burrows, making it impossible to collect those samples (Panaino, 2021). Additionally, as a result of extensive grass cover associated with higher-than-normal rainfall during the study, the visibility of pangolins and their scat was lower than usual when followed.

Figure 3.4. Temminck's pangolin (*Smutsia temminckii*) defaecation site located within the Tswalu Kalahari Reserve in the Northern Cape province of South Africa. Pangolins also dig a small hole in the soil (although not always) as seen by the image, dropping the sausage-shaped excrement in the hole. They sometimes drag their tail over the faecal matter, thereby burying it under the soil or scattering it along the ground, often making it difficult to detect or collect.

In total, I collected 33 faecal samples from tagged pangolins (Table 3.1). Each scat sample was stored in a resealable plastic packet for later analysis. As done for aardvark scats, I stored each scat sample in a resealable plastic packet for later analysis.

Table 3.1: The number of scat samples collected from aardvark (*Orycteropus afer*) (*n*=93) and Temminck's pangolin (*Smutsia temminckii*) (*n*=33) per month at Tswalu Kalahari Reserve, Northern Cape province, South Africa (indicated by the initial letter of each month, in order) from September 2020 to August 2021, and the total number over the year.

	2020						**2021**						Total
Month	S	O	N	D	J	F	M	A	M	J	J	A	
Species													
Aardvark	8	7	6	30	1	7	3	7	7	6	7	4	93
Temminck's pangolin	4	2	2	3	3	3	2	3	1	4	3	3	33

3.2.6.3 Scat preparation and analysis

I used the same method as used by Weyer (2018) and Panaino et al. (2022) to process and analyse the scats. The scats were removed from their plastic bag and left to air-dry naturally until each sample reached a constant mass. Each dry sample was placed in a bucket with 2 L warm water and soaked for 10 to 15 minutes to separate the organic matter (ant and termite body parts) from the inorganic matter (sand). Samples were periodically stirred to agitate the faeces and water mixture. I implemented a circular stirring motion to create turbulence within the water-soil mixture to help dislodge the organic matter from the inorganic matter. The insect body parts, being less dense than the soil, rose on top and were collected. Any vegetable matter was removed. The bucket contents were incrementally poured through a tea strainer (Lion Brand®, 0.5 x 0.5 mm, Bombay Tea Strainers Manufacturing, Mumbai, India) into another container to allow collection of the insect body parts in the tea strainer. The insect body parts were then placed into a Tupperware container with no lid and allowed to dry to constant mass for ~10 days. The Tupperware container was covered by a fine mesh net, secured with weights around the edges, to prevent contamination of the samples. When the samples were dry, I took a

subsample between 0.30 g and 0.33 g of the pangolin sample, and between 0.5 g and 0.7 g of the aardvark sample, as used and validated by Panaino et al. (2022) and Weyer et al. (2020) for analyses.

Each subsample was analysed under a microscope (SMZ800 zoom stereo microscope, maximum magnification 63x, Nikon Instruments Europe B.V, Netherlands) to count and identify the ant and termite head capsules. The subsample was thinly spread onto a transparent petri dish (120 x 20 mm Clear Sterile Polystyrene Petri Dishes, Shang Hai WHB, China) overlying a grid under the dish. Only the ants and termites were identified to genus level using the reference collections of ants and termites collected at Tswalu Kalahari Reserve that was obtained by Dr Frederic Delsuc (University of Montpellier, Montpellier, France) and Dr Hamish Robertson (Iziko South African Museum, Cape Town, South Africa), and a guide on the ants of southern Africa (Picker et al., 2019).

3.3 Data analyses

The data for air temperature, rainfall, grass cover, prey abundance and dietary overlap were summarised according to month and then grouped months into seasons as spring (September to November), summer (December to February), autumn (March to May), and winter (June to August), based on the dietary and climatic variability across the months.

Prey abundance was calculated as the total number of ants and termites sampled along a transect divided by the number of pitfall traps retrieved from that transect (occasionally traps were not retrieved when they were trampled by game in the reserve). Thus, prey abundance is expressed as number per trap, and traps were replicated within transects. I then calculated the percentage contribution of each ant and termite genus by dividing the sum of each genus in a transect per month by the sum of all genera in that transect per month, multiplied by 100. To calculate the percentage contribution of each genus to the diet of aardvark and pangolin, the number of individuals (ant and termite heads) representing each genus counted per scat subsample was divided by the total number of prey items counted in that subsample, multiplied by 100.

I used Microsoft Excel 2016 (Microsoft Windows, USA), Graphpad Prism version 8.0.2 software (GraphPad Software, San Diego, CA), and R (version 3.6.1 (RStudio: Integrated

Development for R studio, PBC, Boston, MA) to curate raw data for analysis and to create graphs. I calculated the month-to-month mean grass cover by first averaging the estimated grass cover per transect, and then averaging the grass cover across all transects for each month. I used a generalised linear mixed model to test the effect of rainfall prior to monthly grass cover. In this model, rainfall was the explanatory variable, and grass cover was the response variable.

To assess whether a lag predicted primary productivity better than the rain that fell during the same month as the transects were conducted, a lag of zero, one, two, or three months prior to each transect was analysed and Akaike Information Criterion (AIC) was used to assess the performance of each model (Appendix, Table A11). It is known that rainfall positively affects vegetation and insect abundance in the Kalahari (Weyer et al., 2020; Panaino et al., 2022), thus I used rainfall as a predictor variable, and as a proxy for primary productivity in the study. An issue with using rainfall as a proxy is that there is a lag between rainfall and primary productivity (Dudney et al., 2017). The model with the lowest AIC was then used in the generalized linear model to test the effects of rainfall on grass cover (Appendix, Tables A11 and A12).

I assessed seasonal variation in prey abundance using a generalized linear model (with a negative binomial link) in R (package “lme4”) (Kuznetsova et al., 2017), with season as a fixed effect and transect number as a random effect. To assess seasonal variation in grass cover, a linear mixed model was used, with season as a fixed effect and transect number as random effect. Where model effects were significant, marginal means were estimated (R package “emmeans”) (Lenth and Lenth, 2017; Lenth et al., 2018) to determine statistically significant differences between seasons. The number of termites that fell into pitfall traps was too low to allow for any statistical analyses, and so termite numbers were used in the selectivity index but not in the models. Thus, ant counts were used as a proxy for prey abundance in the models. The data were tested for normality using residual plots and Shapiro-Wilk tests in R. Results are reported as mean ± standard deviation (SD).

To determine the dietary selectivity of the aardvark and pangolin, Ivlev’s prey selectivity index (Ivlev, 1961) was used as in [Equation 3.1] below:

$$E = \frac{\mathrm{r}-\mathrm{p}}{\mathrm{r}+\mathrm{p}}, \quad \text{[Equation 3.1]}$$

where r is the proportion of each prey genus that was identified in the scat and p is the proportion of the prey genus that was in the pitfall traps in the study area. The calculations were performed manually for each genus and for each mammalian species using Microsoft Excel (Microsoft Windows, USA). The values for Ivlev's index range from -1 to 1, where values near 1 indicate that the prey genus was selected by the study species in much greater proportion than it was available in the study area (Ivlev, 1961; Strauss, 1979). Conversely, index values near -1 indicate that the prey genus was selected much less than its abundance in the study area (Ivlev, 1961; Strauss, 1979). Prey with index values near 0 were consumed in proportion to their abundance (Ivlev, 1961). Pianka's index in R (package: "pgirmess") (Giraudoux et al., 2018) was used as in [Equation 3.2] below to assess the dietary overlap between aardvark and pangolin (Pianka, 1973; Pianka and Pianka 1976):

$$\alpha = \frac{\sum P_{ia} P_{ib}}{\sqrt{\sum P_{ia}^2 \sum P_{ib}^2}} \quad \text{[Equation 3.2]}$$

where α equals the dietary overlap between α and species b, and Pia is the proportion of prey genus i in the diet of mammal a (aardvark) and Pib is the proportion of prey genus i in the diet of mammal b (pangolin). The values for dietary overlap range from 0 (no overlap) to 1 (complete overlap) (Pianka, 1973). The values for dietary overlap were multiplied by 100 to express them as percentage overlap.

The effect of prey abundance, considering factors such as season, grass cover score, the number of ants, and rainfall, on the dietary overlap (measured using Pianka's index) was tested between the aardvark and pangolin. Due to the limited data available for monthly termite abundance, this factor was excluded for further analysis. Because all the variables are related, I then tested which rainfall variable best predicted the dietary overlap between aardvark and pangolin (Appendix, Table A17). To assess whether a lag of zero, one, two, or three months provided the best estimates for the dataset, I used Akaike Information Criterion (AIC) to determine whether rainfall had the greatest impact on the dietary overlap

between aardvark and pangolin (Appendix, Tables A17 and A18). The model with the lowest AIC was then used in a generalized linear model to test the effect of rainfall (as a proxy for primary productivity) on the dietary overlap between aardvark and pangolin (Pianka's index). Models that had ΔAIC value at least 2 lower than another model were considered superior (Burnham and Anderson, 2004; Burnham et al., 2011).

3.4 Results

3.4.1 Air temperature and rainfall

The mean monthly air temperature at the study site fluctuated during the study period between September 2020 and August 2021 (Appendix, Figure A4), with air temperature reaching an absolute daily maximum of 40 °C during summer (December to February) and an absolute daily minimum of -5 °C during winter (June to August). The annual rainfall during the study was 517 mm, with January being the wettest month with 205 mm (Figure A4). The annual rainfall during the study was higher than the historical average (2001 to 2021, average annual rainfall = 326 ± 130 mm; Tswalu weather records).

3.4.2 Prey abundance, grass cover, and the diet of aardvark and pangolin.

One-way ANOVA showed a statistically significant difference in the abundance of ant prey (measured as ants per trap) between seasons ($P < 0.05$) (Appendix, Figure A5; Tables A15 and A16). The mean prey abundance of ants was higher during autumn, with 54.0 ± 77.1 ants per trap, and winter, with 35.0 ± 34.3 ants per trap, than it was during summer, where there were 23.0 ± 12.4 ants per trap, and during spring, where there were 14.0 ± 12.0 ants per trap (Figure 3.5). Statistically, the mean ant abundance per trap during summer was lower than during autumn ($P < 0.05$), the mean ant abundance per trap during summer higher than during spring ($P < 0.05$), the mean ant abundance per trap during summer was lower than during winter ($P < 0.05$), while the mean ant abundance per trap during winter was higher than during spring ($P < 0.05$).

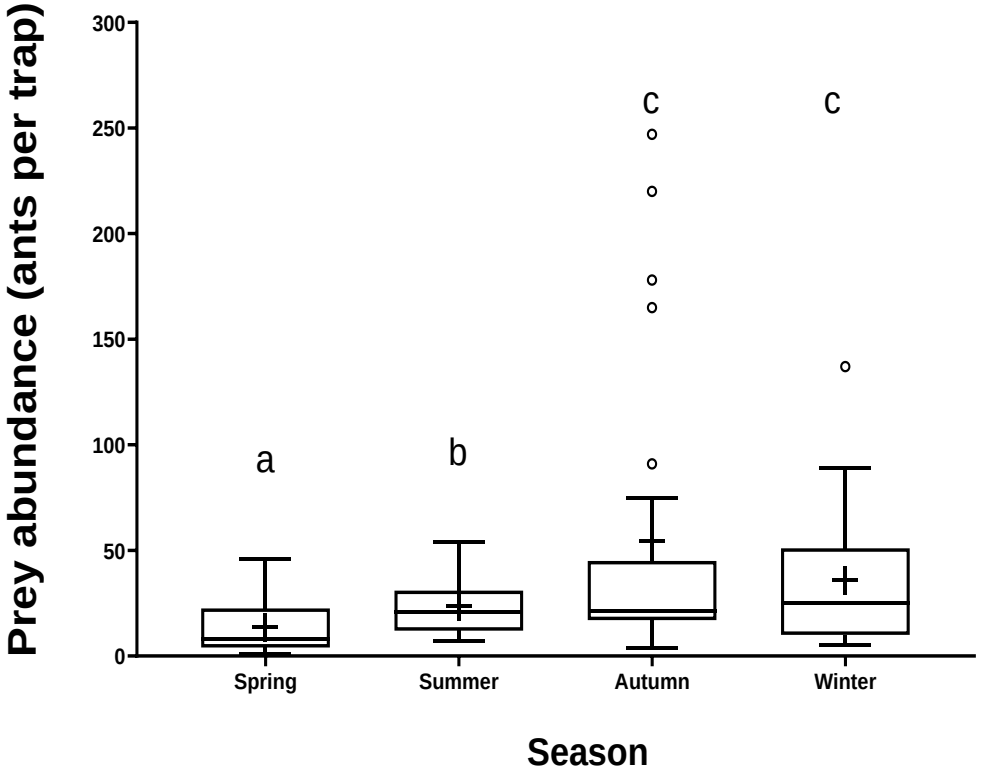

Figure 3.5: Ant capture per trap, in each season across the study period (between September 2020 to August 2021) at Tswalu Kalahari Reserve, Northern Cape province, South Africa showing the minimum and maximum (bars) values. The horizontal line spanning each box represents the median value and the cross sign in each box represents the mean value. ° Indicates outliers. Bars with different superscripts indicate significant differences, while bars with the same superscript do not. [a]Ant prey abundance during spring was lower than ant prey abundance in all seasons ($P < 0.05$). [b] Ant prey abundance during summer was significantly higher than ant prey abundance in spring ($P < 0.05$) but lower than ant prey abundance during autumn and winter ($P < 0.05$). Ant prey abundance during autumn and winter was higher than ant prey abundance during spring and summer ($P < 0.05$).

There was a statistically significant difference in grass cover score between seasons ($P < 0.05$). On average, the mean grass cover score during autumn was 20.2 ± 12.8, and the

mean grass cover score during winter was 19.8 ± 14.4, and both were higher than the mean grass cover score during spring (8.0 ± 7.3) and the mean grass cover score during summer (2.7 ± 3.5) (Figure 3.6; Appendix Tables A13 and A14). Statistically, the mean grass cover scores during autumn and winter were higher and significantly different to mean grass cover scores during spring and summer ($P < 0.05$), the mean grass cover score during summer was lower than that during autumn ($P < 0.05$), the mean grass cover score during summer was lower than during spring ($P < 0.05$), the mean grass cover scores during spring and summer were lower than the scores during autumn and winter ($P < 0.05$) , while grass cover scores were not statistically different between autumn and winter ($P > 0.05$).

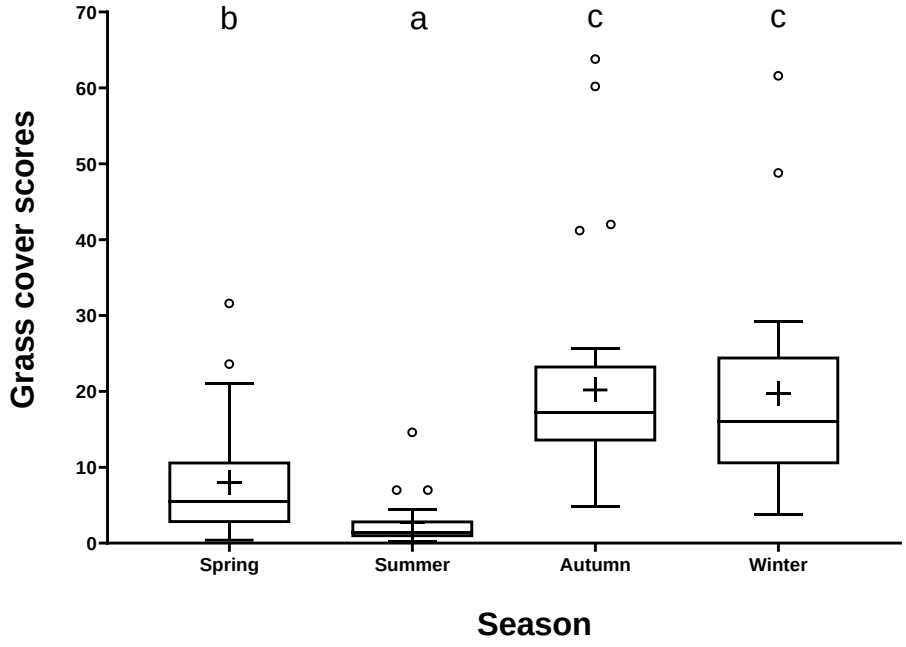

Figure 3.6: Seasonal grass cover scores between September 2020 and August 2021 at Tswalu Kalahari Reserve, Northern Cape province, South Africa showing the minimum and maximum (bars) values. The horizontal line spanning each box represents the median and the cross in each box represents the mean value. ºIndicates outliers. Bars with different superscripts are significantly different and bars with the same superscript are not significantly different. [b]Grass cover during spring was significantly higher than during summer ($P < 0.05$ and lower than grass cover during autumn and winter ($P < 0.05$). [a]Grass cover during summer was significantly lower than grass cover in all other seasons ($P < 0.05$). Grass cover during autumn and winter did not differ from each other.

Ants were collected more in the pitfall traps (99.9%) than were termites, which accounted for only 0.1% of the prey species. *Monomorium* ants were the most common contents of the pitfall traps (42%), followed by *Pheidole* ants. (18%), and *Anoplolepis* ants. (16%), while *Anochetus* ants. contributed little to the pitfall traps (0.009%). Of the termites that were captured in the traps, *Trinervitermes* ants. contributeds (0.03%), followed by *Hodotermes* ants. (0.02%), and *Psammotermes* ants. (0.01%) (Table 3.2). Although there was some dietary overlap, the prey genera in the faecal samples differed between the aardvark and pangolin (Table 3.2). Aardvark faeces contained 72% termites and 28% ants, with *Trinervitermes* termites (45%) making the majority of the genera, followed by *Hodotermes* termites (25%), and *Anoplolepis* ants (22%). In contrast, pangolin faeces contained 80% ants and 20% termites, dominated by *Crematogaster* ants (42%), followed by *Anoplolepis* ants (33%), and *Trinervitermes* termites (10%) (Table 3.2).

Table 3.2: Percentage of ants and termites, by genus, in the pitfall traps (*n* = 200 traps every second month) and their percentage contribution to the total contents of aardvark (*n* = 93 faecal samples) and pangolin (n = 33 faecal samples) between September 2020 and August 2021 at Tswalu Kalahari Reserve, Northern Cape province, South Africa.

Genus	**Pitfall trap (%)**	**Aardvark faeces (%)**	**Pangolin faeces (%)**
Ants (% Total)	99.9	27.7	79.6
Anochetus	0.009	–	–
Anoplolepis	16.4	21.7	32.8
Camponotus	0.2	0.8	2.8
Crematogaster	1.5	0.2	42.3
Dorylus	0.0	0.6	0.01
Lepisiota	2.1	–	–
Monomorium	42.2	0.2	0.2
Ocymyrmex	2.4	0.4	0.3
Tapinolepis	9.4	0.9	0.5
Tapinoma	0.8	–	–

Tetramorium	6.5	2.8	0.5
Tetraponera	0.02	–	–
Pheidole	18.1	0.2	0.2
Plagiolepis	0.3	–	–
Termites (% Total)	0.1	72.3	20.4
Hodotermes	0.02	25.3	10.1
Trinervitermes	0.03	45.4	10.2
Psammotermes	0.01	1.6	0.1

3.4.3 Indices of dietary selectivity and overlap

Ivlev's selectivity index revealed that neither the aardvark nor the pangolin selected the most abundant prey items in the study area (Figure 3.7). Although *Monomorium* ants. (42% of trap contents) and *Pheidole* ant (18%) were the most abundant genera in the traps, they appeared in the scats of aardvark and pangolin in much lower proportions than their abundance (as reflected by a large negative index score: Figure 3.7). *Anoplolepis* ants. were the third-most abundant species captured in the traps (16%) and appeared in the diet in about that same proportion (index near 0) for both the aardvark and pangolin. *Trinervitermes* and *Hodotermes* termites contributed little to the pitfall traps, but aardvark and pangolin both had a high proportion of these genera in their scat (a high positive index score).

Crematogaster ants also contributed little to the pitfall traps but consisted of a moderate proportion in the diet of pangolins. *Crematogaster* ants were not selected by the aardvark. Although Ivlev's selectivity index was 1 for *Psammotermes* ants, this genus represented the lowest percentage in the traps and did not occur frequently in the diet of both aardvarks and pangolins. Similarly, *Camponotus* ants and *Hodotermes* termites also had a score of close to 1 but did not occur frequently in the diet of the pangolin and therefore were also not their main prey items. All other prey genera were largely unselected by both the aardvark and pangolin, as indicated by the very negative index scores (Figure 3.7).

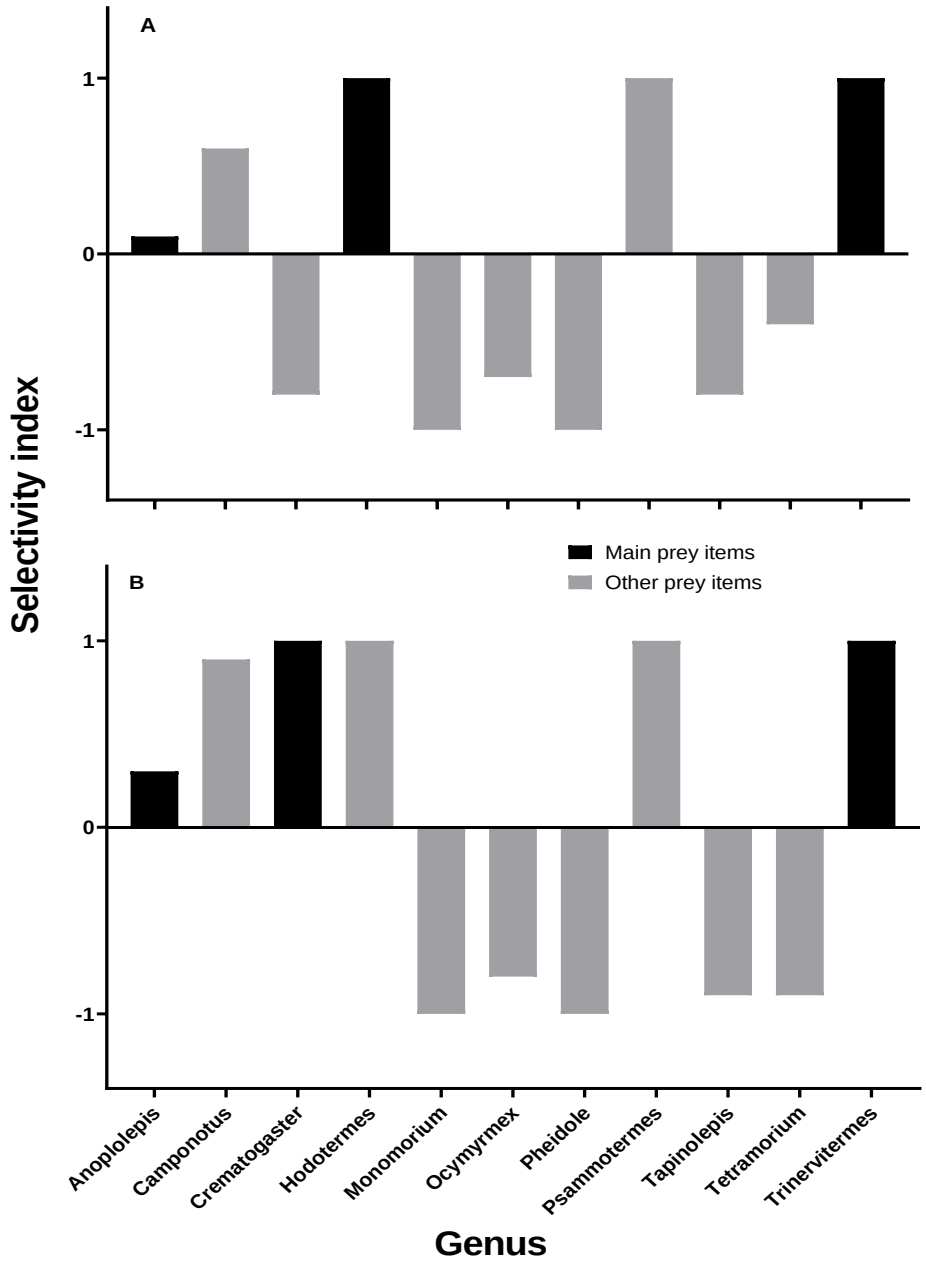

Figure 3.7: Ivlev's selectivity index showing the main prey genera in the scats of aardvark (A) and pangolin (B) (black bars) and other prey genera that were found in the pitfall traps but did not frequently appear in the scats (grey bars) between September 2020 and August 2021 at Tswalu Kalahari Reserve, Northern Cape province, South Africa. *Psammotermes* had a score of 1 but was not the main prey item as it occurred very infrequently in the diet of the aardvark or pangolin. *Camponotus* and *Hodotermes* also had a score of near 1 but did not occur very often in the diet of the pangolin.

There were seasonal shifts in the diet of both the aardvark and the pangolin (Figure 3.8). Aardvarks preyed predominantly on *Trinervitermes* termites during spring (88%) and summer (43%), and *Hodotermes* termites during autumn (50%) and winter (47%). Pangolins preyed predominantly on *Crematogaster* ants during spring (62%) and winter (51%), and mainly on *Anoplolepis* ants during summer (60%) and autumn (48%).

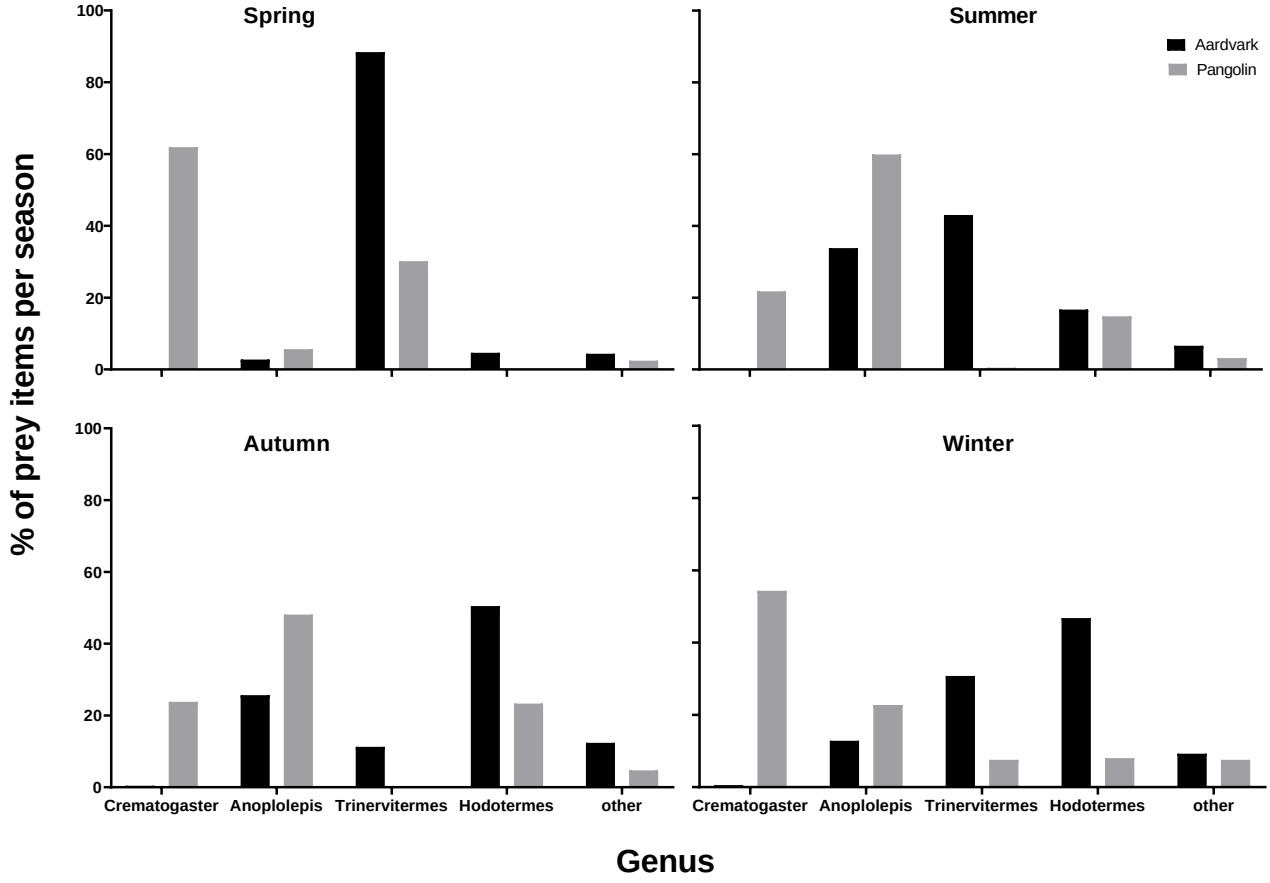

Figure 3.8: Percentage contribution of prey items to the diet of aardvark and pangolin per season between September 2020 and August 2021 at Tswalu Kalahari Reserve, Northern Cape province, South Africa. “Other” includes *Tapinolepis, Tetramorium, Pheidole*, *Monomorium, Ocymyrmex, Camponotus*, and *Dorylus* ants, and *Psammotermes* termites.

The extent of dietary overlap between the aardvark and pangolin varied between seasons (Appendix, Figure A6). It was highest during autumn (67%) and lowest during spring (44%), which coincided with the highest and lowest prey abundance periods, respectively (Figure 3.9).

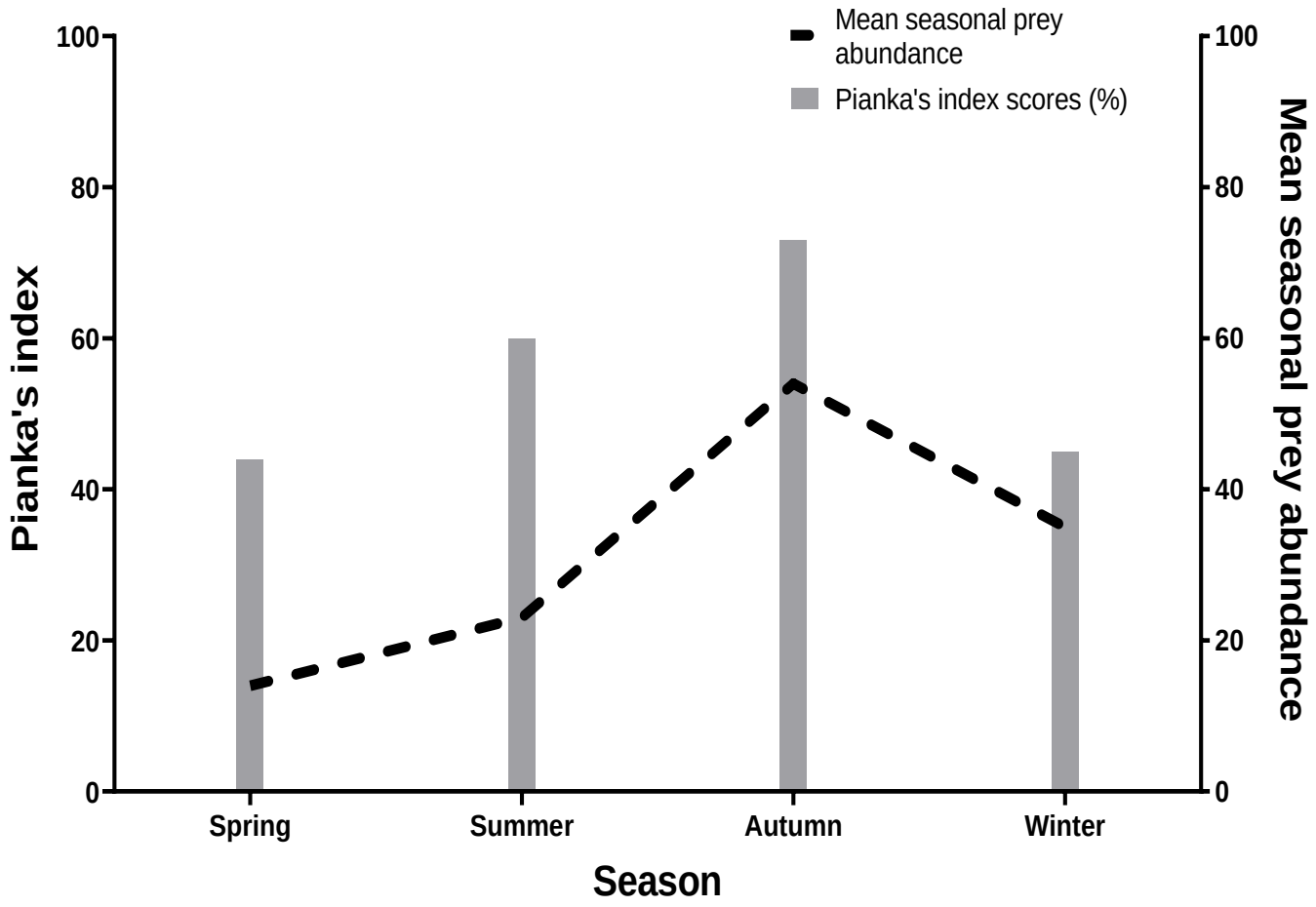

Figure 3.9: Pianka's index (grey bars) for seasonal dietary overlap between aardvark and pangolin (index scores are expressed as a percentage) and the mean seasonal prey abundance (black dashed line) between September 2020 and August 2021 at Tswalu Kalahari Reserve, Northern Cape province, South Africa.

3.4.4 The relationship between rainfall and dietary overlap

The model that included rainfall that fell two months prior to the collection of scats as an explanatory variable to determine prey abundance in the diet produced a lower AIC value than the models that used rainfall that fell during the same month, or one-, or three-months prior. Rainfall two-months prior was therefore used to assess the effect of rainfall on the dietary overlap between aardvark and pangolin (Appendix, Tables A17 and A18). The linear mixed model revealed that rainfall was positively associated with dietary overlap, such that when rainfall increased, so did the dietary overlap between aardvark and pangolin (Figure 3.10 and Appendix, Tables A18 and A19).

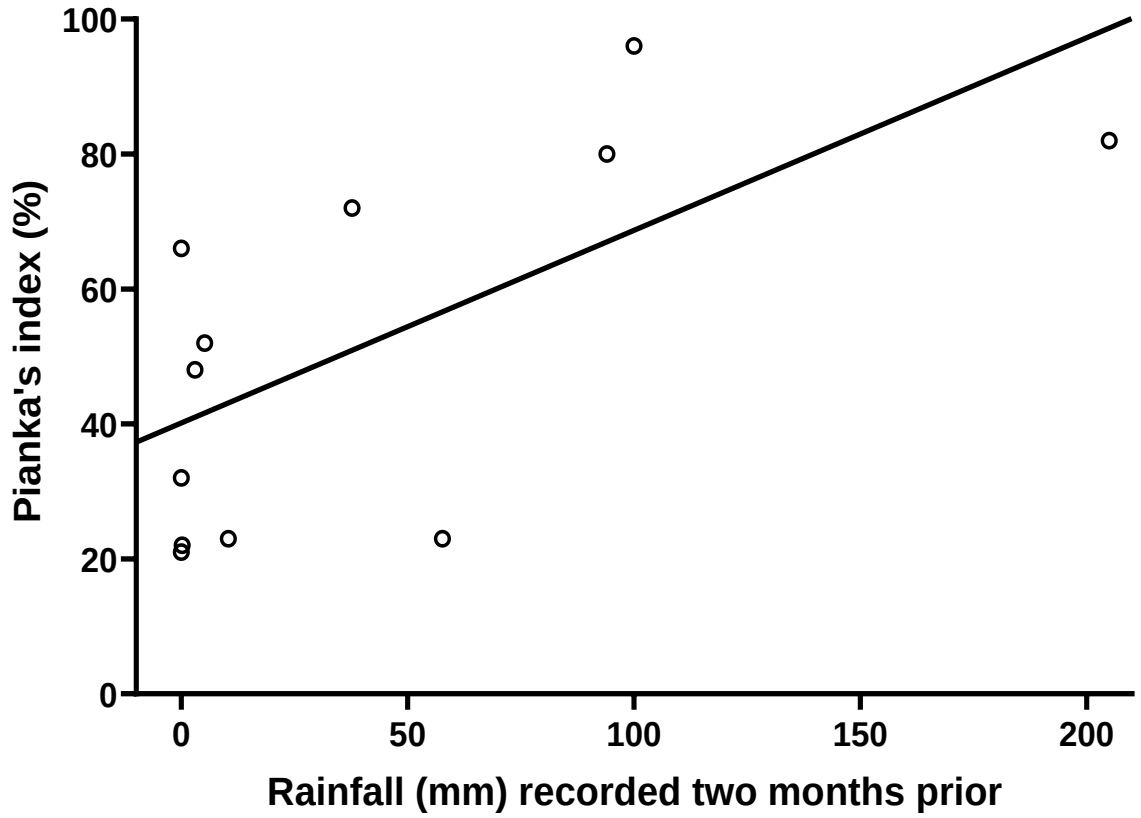

Figure 3.10: The relationship between the amount of rainfall recorded two months prior and the degree of dietary overlap as reflected by Pianka's index, within the studied environment ($P < 0.05$; Y = 0,2794*X + 39,47) between September 2020 and August 2021 at Tswalu Kalahari Reserve, Northern Cape province, South Africa.

3.5 Discussion

I assessed the indices of prey selectivity and dietary overlap to examine potential dietary competition between aardvark and pangolin over a year between September 2020 and August 2021 at Tswalu Kalahari Reserve, Northern Cape, South Africa. Aardvark preyed predominantly on three insect genera, *Trinervitermes* and *Hodotermes* termites, and *Anoplolepis* ants. Pangolin preyed predominantly on *Crematogaster* and *Anoplolepis* ants, and *Trinervitermes* termites. *Monomorium* ants were the most frequently captured ants in the pitfall traps, followed by *Pheidole* ants, yet these genera were found in low percentages in the scats of both aardvark and pangolin. Aardvark preferred *Trinervitermes* termites during spring and summer and *Hodotermes* termites during autumn and winter. The

pangolin preferred *Crematogaster* ants during winter and spring and *Anoplolepis* ants during summer and autumn. The seasonal change in dietary preference of aardvark and pangolin resulted in varying degrees of dietary overlap between these two mammalian species, with the dietary overlap appearing to be related to primary productivity (rainfall). When rainfall was high, and hence when food abundance was high, the dietary overlap between aardvark and pangolin was high. In contrast, when rainfall was low, and hence food was less abundant, the dietary overlap was lower. Some dietary overlap occurred during all seasons.

A previous study that compared the diets of the two mammalian species, with data collected from different regions, and at different times, revealed a moderate degree of overlap (dietary niche breadth 0.49–0.57) between the aardvarks and pangolins (Pietersen and Robertson, 2023). The data, collected from studying the diets of these two species at the same time and in the same environment, suggests a potentially greater dietary overlap at certain times of the year. While the present study demonstrates that the dietary overlap studied simultaneously is different than what has been inferred in separate studies on each species conducted at different times and in different areas (Lindsey, 1999; Taylor et al., 2002; Prediger, 2020; Pietersen and Robertson, 2023), the results in the present study might also specifically reflect patterns in prey abundance that occur in years with above-average rainfall or regional differences, considering that the study used averaged values across the whole of southern Africa (Pietersen and Robertson, 2023). In the present study, the annual rainfall exceeded 500 mm, which was about 1.6 times more than the recent historical average for the study site. Whether the pattern identified in the present study is more generalisable to other years, and particularly during drier years, will require further study. Another limitation of the present study is that the data on ant and termite abundance were collected using pitfall traps only, which likely underestimated the abundance of arboreal species such as *Crematogaster* ants, and subterranean species, particularly termites. Termite numbers were particularly low in the traps than termite numbers that were previously recorded in the same traps under the same environment (Sattar et al., 2013; Mitchell et al., 2019; Thabit et al., 2019), possibly as a result of the impacts of a severe drought period before the present study on termite populations (Phakoago MV, personal observation).

While prey abundance was assessed at a bi-monthly interval and over a year, which should be adequate to detect overall trends in prey abundance (Wolda, 2004; Cardoso and Leather, 2019), the present study collected relatively few scats from pangolins, despite tracking the animals with telemetry. The limited dataset therefore might not provide conclusive insights into the dietary preferences of both aardvark and pangolin. Monthly assessments of prey abundance would have been better to draw robust conclusions on the monthly abundance of prey species and diet selectivity for both aardvark and pangolin. In addition, my team's previous research experience indicated that the number of scats collected was sufficient to provide adequate results according to seasons. However, it would be beneficial to confirm this idea by constructing sample size by diet diversity curves to ensure that diet diversity levels off with the available sample sizes, in future. Nevertheless, given the strong link between rainfall, grass cover, and prey abundance in the Kalahari (Jeltsch et al., 1999; Pietersen et al., 2016; D'Onofrio et al., 2019; Meyer et al., 2019; Panaino et al., 2022), the present study was able to link primary productivity (using rainfall as a proxy) to the extent of dietary overlap between the aardvark and pangolin.

In the present study, the aardvark showed a preference for three primary prey items, and these preferences varied seasonally. Aardvark consumed *Trinervitermes* termites in greater proportion during spring and summer than during autumn and winter, apparently switching preference to *Hodotermes* termites during the autumn and winter. The aardvark consumed *Anoplolepis* ants more during the rainy season during summer than in the other seasons. In contrast, a study conducted in the Karoo reported that the *Anoplolepis* ant was consumed more during winter than during summer (Willis et al., 1992), while a study conducted in the Natal highlands reported that *Dorylus* ant was preferred during summer (Melton and Daniels (1986). Overall, the *Trinervitermes* termite was the main prey item consumed by the aardvark in the present study. In contrast, a study conducted in the same area from 2012 to 2015 reported that the *Hodotermes* termite was the main prey item of the aardvark in all seasons (Weyer et al., 2020). In the Karoo region, the *Anoplolepis* ant was the preferred prey item during both summer and winter (Taylor et al., 2002). The findings of the present study may have differed because of the unusually wet year during

the present study period, or the drought period that preceded the study, or because the Kalahari area is different to the Karoo.

The shift in primary prey items across seasons may be attributed to changes in resource availability, environmental conditions, or physiological needs of animals. *Trinervitermes* termites are adapted to wetter conditions, potentially making them easier for aardvarks to access during summer, while *Hodotermes* termites exhibit more surface activity during winter and adapt to drought with deeper, more water-efficient burrows (Hatwig, 1965; Pietersen et al., 2016). The population dynamics of *Hodotermes* termites show build-ups after successive dry years and declines after periods of above-average rainfall (Mitchell et al., 2019). *Hodotermes* prefer dry grass and wood, with increased activity during winter (Zachariassen et al., 1988; Duncan and Hewitt, 1989), potentially leading aardvarks to shift their feeding preferences during this season. In the Kalahari, spring and summer are characterized by higher temperatures, rainfall, and insect activity compared to autumn and winter (Pietersen et al., 2016; Adam et al., 2018; Weyer et al., 2020; Panaino et al, 2022).

In the present study, pangolins showed a preference for three primary prey items, and the preference for those prey items varied seasonally. The pangolin consumed *Crematogaster* ants during winter and spring and switched to *Anoplolepis* ants during summer and autumn. Overall *Crematogaster* was the main prey item consumed by pangolins in all seasons, consistent with previous studies conducted in the same Kalahari region between 2013 and 2017, even though the *Crematogaster* ant contributed little to the pitfall traps (Pietersen et al., 2016; Panaino et al., 2022). Some of the *Crematogaster* ants are arboreal (Richard et al., 2001; Tschinkel, 2002) and are thus less likely to fall into pitfall traps than are ground-dwelling insects (Picker et al., 2019), making it challenging to assess these factors when using only pitfall traps for *Crematogaster* abundance.

Although the study was conducted over one year, during the summer and autumn following high rainfall, pangolins increased their consumption of *Anoplolepis* ants, when activity of these ants was high compared to spring and winter, as reflected by counts in the pitfall traps. Higher *Anoplolepis* ant activity during summer compared to winter has been reported in the Lowveld area of South Africa (Swart et al., 1999). The impact of environmental factors, such as rainfall, on the foraging behaviour of pangolins highlights the complexity

of their dietary preferences and adaptive strategies (Richer et al., 1997; Prediger, 2020). During winter or when conditions become very dry*, Anoplolepis* ants retreat deep into their underground colonies, as indicated by their decreased abundance in the pitfall traps, making them inaccessible to surface foragers (Addison and Samways, 2000; Kuate et al., 2008).

Some mammals shift their diet to different species during winter to compensate for a reduction in prey resources (Williams et al., 1997; Klare et al., 2011), most likely to allow them to maintain energy intake through winter. Dietary shifts over seasons also may be an attempt by the pangolin and aardvark to increase water intake, as they drink rarely (Phakoago et al., 2024), but this requires further investigation. While the daily energy and water intake was not estimated in the present study, it would be recommended for future studies to determine the energy and water content of the preferred prey items of the aardvark and pangolin.

Although the mammalian species in the study had clear preferences for specific prey items, and displayed a degree of dietary overlap when I assessed their diets simultaneously and under the same climatic conditions. There was some degree of dietary overlap in all seasons, with higher overlap when resources were more abundant during autumn, and lower dietary overlap when resources were less abundant during spring. The high abundance of food resources (ants) in the study during autumn was likely a direct result of above-average rainfall in the preceding summer, as shown by Pietersen et al. (2016) for ant activity in their study during autumn. A positive association between rainfall and dietary overlap was evident; as rainfall increased, the dietary overlap also increased as assessed using Pianka's Index. When food was more abundant, the dietary overlap of aardvark and pangolin in the present study was high (73%), whereas Pietersen and Robertson (2023) used published data from different regions and reported 57% dietary overlap between aardvarks and pangolins. The differences in dietary overlap observed between these studies may be attributed to various factors, including the availability of resources, habitat characteristics, and the specific feeding behaviours of the animals.

In general, more available food resources tend to lead to increased dietary overlap, as species can afford to be less selective (Chesson, 2000). However, aardvarks and

pangolins are obligate specialists, with associated morphological adaptations, and as such they cannot vary their diet to reflect the abundance of different prey items. Even with increased dietary overlap, some level of niche differentiation and resource partitioning may still occur to reduce direct competition and maximises overall resource utilisation within an ecosystem (Matich et al., 2017). In addition, during times of low resource abundance species may extend diets to include other food items to meet specific dietary requirements (Perry and Pianka, 1997).

The increased rainfall during summer in the study led to greater grass cover during autumn and winter, likely resulting in an increase in prey resources. Ants and termites, which are preyed on by many Kalahari species, depend on grasses for survival (Weyer et al., 2020; De Almeida et al., 2020; Panaino et al., 2022; Parr and Bishop, 2022). As grass depends on rainfall for its growth and survival, it was expected that rainfall would be a good predictor of both grass cover and the abundance of ants and termites. In the present study, prey abundance correlated positively with grass cover, with the highest grass cover occurring during autumn and winter, two months after the rainfall peaked in January.

During periods of low rainfall, vegetation becomes scarce, reducing food abundance for insects, leading to decreased ant and termite populations (Weyer et al., 2020). Contrary to expectations, I found higher grass cover and prey abundance during autumn and winter compared to during spring and summer. The difference is likely due to substantial summer rainfall, particularly in January, which led to increased prey abundance during autumn. Rainfall from preceding months impacts insect abundance and vegetation composition in arid ecosystems (Dudney et al., 2017; van de Ven et al., 2020; Panaino et al., 2022). The peak in prey abundance during autumn, instead of summer, may be explained by insects moving deeper underground to avoid summer heat (Williams and Middleton, 2008; Dudney et al., 2017).

Prey abundance can considerably influence the dietary preferences of predatory species across the year. Aardvark and pangolin have demonstrated the ability to adapt their foraging strategies in response to fluctuations in prey abundance (Burton-Roberts et al., 2022). While these species primarily target specific prey items, they can shift their focus to alternative food sources when their typical prey becomes scarce (Kaiser and Franz-

Odendaal, 2004). The only prey item that was consumed in proportion to its abundance was *Anoplolepis* ants. Based on scat analysis, 34% of the aardvark diet and about 60% of the pangolin diet comprised of *Anoplolepis* ants, when these ants were most abundant after summer rains, indicating that *Anoplolepis* ants are an important food source for both aardvarks and pangolins. Similarly, *Anoplolepis* ants constituted a significant portion of the pangolin's diet, comprising more than 70% of their food intake in a study conducted in the Lowveld of South Africa (Swart et al., 1999; Pietersen and Robertson, 2023). The high calorific value (Taylor, 1998; Panaino, 2020) of *Anoplolepis* ants likely makes them essential for meeting the energy requirements of aardvarks and pangolins. Nutritional challenges for the aardvark and pangolin may occur during droughts when this prey species becomes less abundant (Lindsey and Skinner, 2001; Taylor et al., 2002; Panaino et al., 2022).

Trinervitermes termites lack cuticular pigmentation and consequently are not active during the day (Hewitt et al.,1972). They are also inactive when ambient temperature is below 9 ºC (Richardson, 1987) and thus they are largely unavailable to the aardvark during winter. On the contrary, if insects are inactive and clumped in their nests, they could present a concentrated and energetically rewarding food resource for aardvarks. However, it is more likely that the hard exterior of the epigeal mounds prevents aardvarks from exploiting these resources. The structural integrity and hardness of these mounds make it difficult and energetically costly for aardvarks to break into them, deterring access to the clumped insect resources during the winter months. The aardvark scats consisted of close to 90% *Trinervitermes* termites during spring but only 30% during winter. Aardvark scat comprised about 46% *Hodotermes* termites during winter probably because *Hodotermes* termite become active on the surface during winter, and it is energetically less demanding to forage at a *Hodotermes* feeding port in sand than it is to dig through the hard exterior of an epigeal *Trinervitermes* mound. Such a diet switch of the aardvark is not unprecedented, with a similar switch from *Trinervitermes* termites to *Hodotermes* termites being reported for aardvark in the Nama Karoo (Willis et al., 1992). Another myrmecophagous mammal, the aardwolf, also switched to *Hodotermes* termites during winter from *Trinervitermes* termites during summer (Williams et al., 1997). The switch reflects differences in the activity patterns and abundance of these termite species to their predators

Overall, ants and termites of the genera *Trinervitermes, Hodotermes, Crematogaster*, and *Anoplolepis* were the most predominantly preyed upon items for aardvark and pangolin, but they were not the most abundant in the pitfall traps of the present study. The prey items were likely abundant to aardvark and pangolin because of the nature of their nesting or foraging habits. On the other hand, the ant genera *Tapinolepis, Tetramorium, Pheidole, Monomorium, Ocymyrmex, Camponotous*, and *Dorylus,* and the termite genus *Psammotermes*, had low occurrence in the pitfall traps and appeared only a few times in the scats of the aardvark and pangolin. These insect genera were likely ingested incidentally when aardvark and pangolin were feeding on their preferred prey items. The selectivity index in the present study revealed that neither the aardvark nor the pangolin selected the most abundant prey items that were available to them. Thus, a distinction must be drawn between prey availibility that focuses on the presence and accessibility of potential prey, and prey abundance that quantifies the actual number or density of prey individuals within a specific area (Redford, 1987; Pietersen et al., 2016b).

In summary, the aardvark and Temminck's pangolin showed a high level of dietary overlap when resources were abundant during autumn but less dietary overlap when resources became scarce during spring. The higher dietary overlap during autumn than in the other seasons may be the result of unseasonal rain in late summer, and the rainfall lag effect. Rainfall two months prior best predicted grass cover in the present study, and grass cover was associated with ant and termite abundance. The results in the present study may have also been influenced by the unusually wet year in the Kalahari, which would have resulted in higher food abundance overall for the aardvark and pangolin. Whether niche partitioning occurs to the same extent in drier years remains to be determined. If prey is abundant, multiple species may share diets without competing (Whitfield et al., 2013; Pietersen and Robertson, 2023). Even when prey is less abundant, predators may be separated by foraging ecology, and spatial or temporal differences in resource use (Jones and Barmuta, 1998; Kronfeld-Schor and Dayan, 1999; Browning et al., 2014; Pietersen and Robertson, 2023). More investigations are needed to further understand both the degree of dietary overlap between these two mammalian species as well as the underlying mechanisms that facilitate the overlap.

Chapter 4 - The use of burrows as a way for animals to buffer the energetic-cost of winter in the Kalahari

4.1 Introduction

Burrows are critical resource for many species because they provide microhabitats that are suitable to escape harsh environmental conditions (Bao et al., 2013; Pietersen, 2013). They also act as a refuge, allowing animals to avoid predators and provide a safe environment in which to raise the young (Whittington-Jones, 2006; Pietersen, 2013; Haussmann et al., 2018; Weyer, 2018). In drylands where air temperatures are high during the day, and likely to increase with future climate change (Tadross et al., 2011; van Wilgen et al., 2016), heat loads may fluctuate substantially across the diel cycle, and seasonally (Lowney et al., 2020; Fuller et al., 2021). During the day, air in an occupied burrow is usually more humid than the air above-ground, which reduces the gradient for evaporative water loss, and thus animals lose less water while they are in the burrow than outside. Burrow use also reduces exposure to high solar radiation, allowing animals to conserve body water that would otherwise be used for evaporative cooling (Fuller et al., 2021).

To maintain homeothermy, mammals must either retreat to warmer microclimates, use energy through shivering or non-shivering thermogenesis, or increase activity in the face of a heat sink at night (Fuller et al., 2021). Taking refuge in a burrow reduces heat loss to the environment and the energetic demands of thermoregulation (Taylor and Skinner, 2004; Whittington-Jones et al., 2011). Burrows therefore provide thermally buffered microclimates (Whittington-Jones et al., 2011) and facilitate energy and water savings through reduced costs of thermoregulation (Pietersen, 2013).

Two species that use burrows are Temminck's pangolin and the aardvark (Whittington-Jones, 2006; Pietersen, 2013; Haussmann et al., 2018; Weyer, 2018). Recent evidence from the Kalahari shows that the aardvark is under energetic stress during winter, particularly when food is scarce and following periods of either drought or low rainfall (Rey et al., 2017; Weyer et al., 2020). To reduce the energetic costs of staying warm it might be expected that during cold weather, the aardvark and pangolin would select the warmest burrows that are available in their environment. The subsequent warming of the burrow will play a key role in the burrow temperature, and thus on energy saving that an animal might make (Chappel and Bartholomew, 1981; Fick et al., 2009; Milling et al., 2018).

The orientation of a burrow to the sun influences the amount of solar radiation that penetrates the burrow (Chesemore, 1969). While burrowing animals will go deeper into a burrow than the level that sunlight will penetrate, the orientation of the burrow can help animals to avoid exposure to direct solar radiation during the hottest part of the day (Whittington-Jones et al., 2011; Pike and Mitchell, 2013; Holtze et al., 2018; Singh, 2018). In the southern hemisphere, the angle of incoming solar radiation is generally higher on north-facing slopes compared to south-facing slopes (Gallardo- Cruz et al., 2009). In the northern hemisphere, some species of burrowing rodents, such as kangaroo rats (*Dipodomys spectabilis*) and pocket mice (*Perognathus flavus*), avoid sun exposure and construct burrows with entrances that face either to the north or northeast, which helps to reduce exposure to direct sun rays during the hottest part of the day (Johnsgard, 2003). In an alpine region in Canada in the northern hemisphere, animals preferred east and south-facing slopes, compared to north- and west-facing ones (Hall and Lamont, 2003). Alpine marmots (*Marmota marmota*) preferred south and east facing slopes (Lenti-Boero, 2003). Among the 51 burrows of the Himalayan marmot (*M. himalayana*), 20% had a south-facing orientation, 30% had a southwest facing dimension and 50% were oriented to the west (Wang and Hou, 2021). The entrance to Arctic fox (*Vulpes lagopus*) burrows had either a southerly, easterly, or westerly orientation and rarely a northerly dimension possibly indicating a preference for burrows that capture solar radiation in the northern hemisphere (Chesemore, 1969; Rangwala et al., 2013).

Aardvarks and pangolins use burrows in sandy areas and the two species are never found in areas where they are unable to dig burrows (Whittington-Jones et al., 2011; Pietersen et al., 2014; Martin, 2017). In areas where dunes are present, such as the Kalahari, both species prefer to use burrows on dune slopes rather than on flat terrain (Whittington-Jones 2006; Pietersen, 2013; Rey et al., 2017; Weyer, 2018; Panaino, 2021). Dunes tend to have a looser, more porous soil structure than flat terrain, which makes it easier to dig burrows (Herbst and Bennet, 2006).

Another factor that may influence the preference of an animal for its burrow is food availability. Aardvarks and pangolins feed on ants and termites, which are associated with grass cover as these insects feed on the grass (Moll et al., 2012; Wills and Landis, 2018).

The grass cover provides a suitable habitat in terms of shade and moisture for ants and termites (Wehner and Wehner, 2011; Geerts et al., 2016; Silva et al., 2017). Seasonal changes in vegetation productivity led to changes in grass cover over the year, with productivity being highest during summer (Pietersen et al., 2014; Tokura et al., 2018; Weyer, 2018; Panaino et al., 2022). The characteristics of grass cover (species, height, and biomass) have been shown to have an important influence on burrow selection in small mammal species such as marmots and squirrels (Ewacha et al., 2016; Li et al., 2017). Whether the position and orientation of the burrows that are used by aardvark and pangolin is influenced by grass cover, and the likely associated prey base, is unknown. I therefore investigated how active burrows are distributed between areas with differing grass cover (resulting from differences in historical land use within the reserve), and whether the aardvark and pangolin preferentially build their burrows in either the dune or the dune street (interdune) areas. I also measured burrow temperature, the orientation of the entrance of active burrows, and the orientation of burrows that were not active but were known to have been used by pangolin. It was hypothesised that the density of burrows would be higher in the areas with higher grass cover, which is associated with better prey availability (Bylo et al., 2014; Martin, 2017). It was also hypothesized that the density of burrows would be higher on the dunes than in the dune street areas.

4.2 Materials and methods

4.2.1 Study area

Details of the study area are given in section 2.2.1 in Chapter 2. The Korannaberg section of the reserve, where the study was conducted, is characterized by sandy dunes that run from north to south, interspersed with dune streets. For my study, the Korrannaberg section was divided into two sections that were characterized by different levels of grass cover, termed Northern Tswalu (that had historically been overgrazed) and Southern Tswalu (that had not been overgrazed). Previously, studies in Northern Tswalu as part of long-term monitoring of ants and termites have been undertaken. Between 2016 and 2017, Tswalu Kalahari Reserve purchased additional farmland to the south, and in 2019 the fences in the south were removed. As a result, the south area, known as Southern Tswalu, had not been grazed for some time and consequently had higher grass cover than Northern Tswalu. The duneveld and plains shrubveld habitat types in the Korannaberg

section were selected as the survey area for this study due to the presence of freely roaming aardvark and pangolin.

4.2.2 Air temperature and rainfall

Air temperature and rainfall details are give in section 2.2.2 in Chapter 2.

4.2.3 Burrow transects

A systematic sampling design was used to detect and survey aardvark and pangolin burrows across the duneveld area at Tswalu Kalahari Reserve (~191 km^2), the area where both mammals commonly occur. A vegetation map was converted from a geographic coordinate system to a projected coordinate reference system (EPSG:32734, WGS 84 / UTM zone 34S) in QGIS (version 3.18.3), with the duneveld vegetation type made into a separate shapefile using the feature selection tool. Non-accessible areas on the reserve were cropped out of the shapefile. The resultant duneveld map was imported into Distance software, version 7.3, release 2 (Thomas et al., 2010), where a 1 km^2 grid was overlaid (Figure 4.1). A systematic grid point sampling design was chosen to generate random locations for 61 points that were evenly distributed across the duneveld, spaced approximately 2 km apart, and using minus sampling constraints (Figure 4.1). The 61 generated point coordinates were transformed back into a geographic coordinate system for easy use, using an online transformation platform. The transects were surveyed in July 2021 over 12 days.

Each transect on the map was surveyed by two observers in a pseudo circuit design so that observers finished parallel to their starting point (Stober et al., 2017) (Figure 4.2). Global Positioning System (GPS) (Garmin eTrex 10 outdoor GPS-yellow, Multinational Technology Company, Kansas, USA) coordinates were taken at the start and end of each transect.

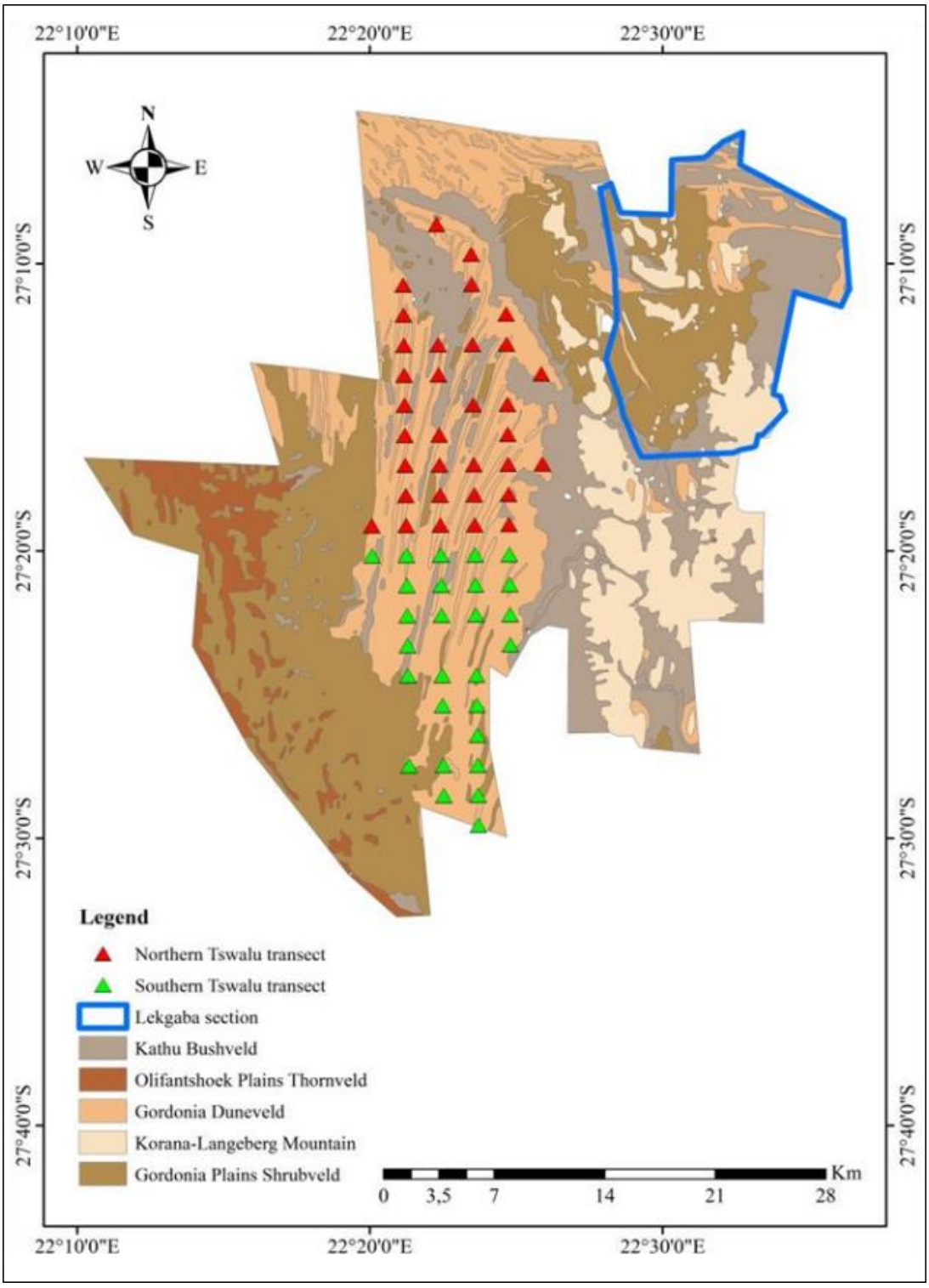

Figure 4.1: Map of Tswalu Kalahari Reserve, Northern Cape province, South Africa showing the Korannaberg section (all except the Lekgaba section - blue boundaries) and the transects (Northern Tswalu - red triangles and Southern Tswalu - green triangles) overlaid on various vegetation types.

The two observers walked 500 m simultaneously in parallel from North to South on the western side of the centre line of a dune (or dune street) to identify burrows. The observers then walked 500 m simultaneously in parallel from South to North on the eastern side of the centre line of the same dune (or dune street). From the starting point of a 'dune transect', the dune crest was used as the centre line (green line on Figure 4.2). The width of each transect was 250 m, the transect length was 1 km (500 m forward and 500 m back) and the total area of each transect was 0.125 km^2 (0.25 km x 0.5 km). Across the 61 transects, an area of 7.625 km^2 (61 transects x 0.125 km^2) was covered (Figure 4.2). The distance between surveyed dunes varied between ~350 m and 500 m (Figure 4.2). The transects on the dune streets were not aligned between two transects on a dune; instead, they were undertaken on the dune street at least either 300 m north or south of each transect on a dune (Figure 4.2), following Stober et al. (2017). A total of 31 transects were surveyed on the dunes and 30 transects on the dune streets by assigning every second point as a dune street and identified the nearest dune street to the randomly generated point.

For each transect on a dune street, the observers walked parallel to the dune to help maintain a straight trajectory. Observer 1 (O1 on Figure 4.2) walked approximately 50 m parallel to the centre line of the transect and Observer 2 (O2 on Figure 4.2) walked 50 m parallel to Observer 1. An assumption in the design was that each observer could detect burrows out to ~25 m on either side of their walking line with ease, given that vegetation growth typically reduced burrow detectability beyond 25 m. Therefore, the width for the transects on the dune streets was 250 m (125 m on each side of the transect on a dune street) and the total area of transects on a dune street was 0.125 km^2 (0.5 km x 0.25 km). For the transects on a dune, Observer 1 walked 50 m from the centre line and Observer 2 walked 50 m parallel to Observer 1. Besides the vegetation growth, the steep sloping nature of the dunes made it easier to detect burrows on the dune from a further distance than on transects in the dune street. Therefore, the width of each transect on a dune was 250 m (125 m on either side of the transect line on a dune), and the total area of each transect on a dune was 0.125 km^2 (0.5 km x 0.25 km). The two observers walked together at the same time; while one observer logged a burrow, the other observer waited, to ensure that the same burrow was not recorded by both observers (Figure 4.2).

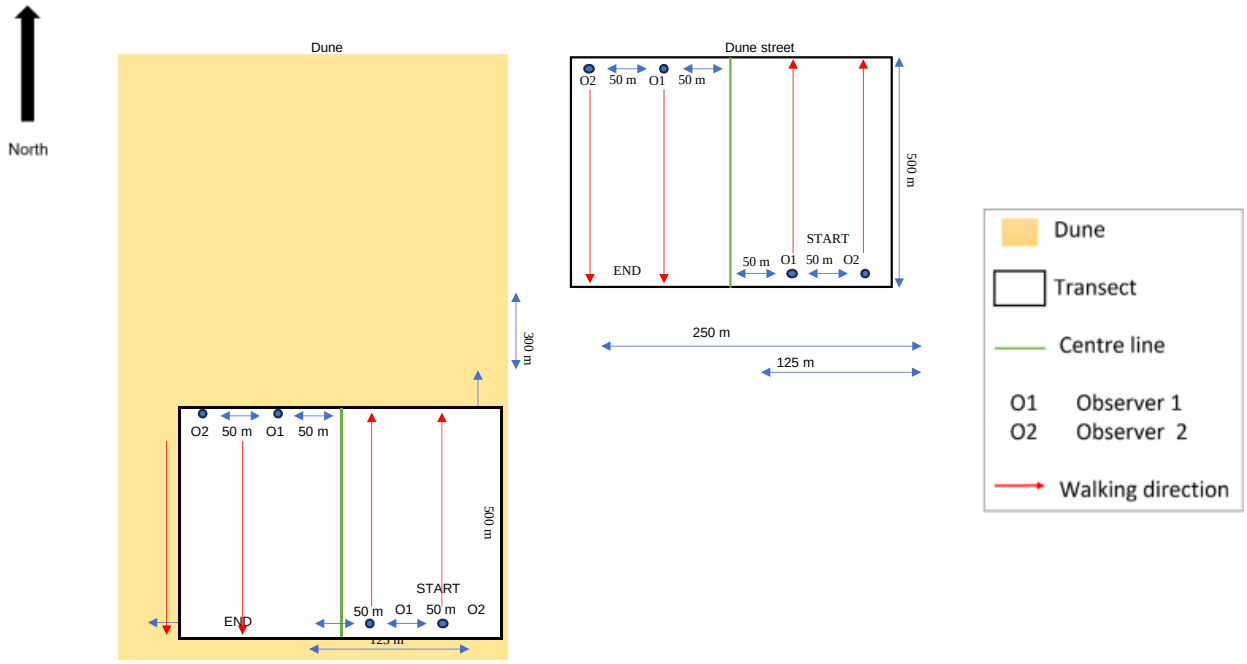

Figure 4.2: Burrow transect design to detect burrows used by aardvark (*Orycteropus afer*) and pangolin (*Smutsia temminckii*) at Tswalu Kalahari Reserve, Northern Cape province, South Africa. O1 indicates the position of Observer 1; O2 indicates the position of Observer 2; blue arrows indicate distances within the transects; red arrows indicate the directions in which observers walked while surveying the transect and green lines indicate the centre line of the transect.

On some of the randomly generated points, either the closest dune or dune street to the point were surveyed. At two of the transects on a dune, there was a known pangolin on the dune; that is one of the pangolins that was tagged with a Very High Frequency transmitter as part of Chapter 3 was detected on that dune, but its exact location was not known. I surveyed the dune to determine whether the burrow transect technique could detect the individual without the use of telemetry. On both transects, the pangolin was detected within the transect by looking for tracks, further ground- truthing that the technique worked for either detecting pangolins or their burrows.

During the surveys, the two observers identified and recorded only active burrows where there was evidence of activity of aardvark or pangolin in the burrow such as fur, footprints, fresh faecal material of aardvark or signs of fresh soil fans outwards away from the burrow.

Burrows were recorded only if the height and width were both > 20 cm, a size that is likely to be adequate for an adult pangolin (Figure 4.3). Old burrows that had either collapsed or were closed off were not recorded. The location of each identified burrow was recorded with a GPS device.

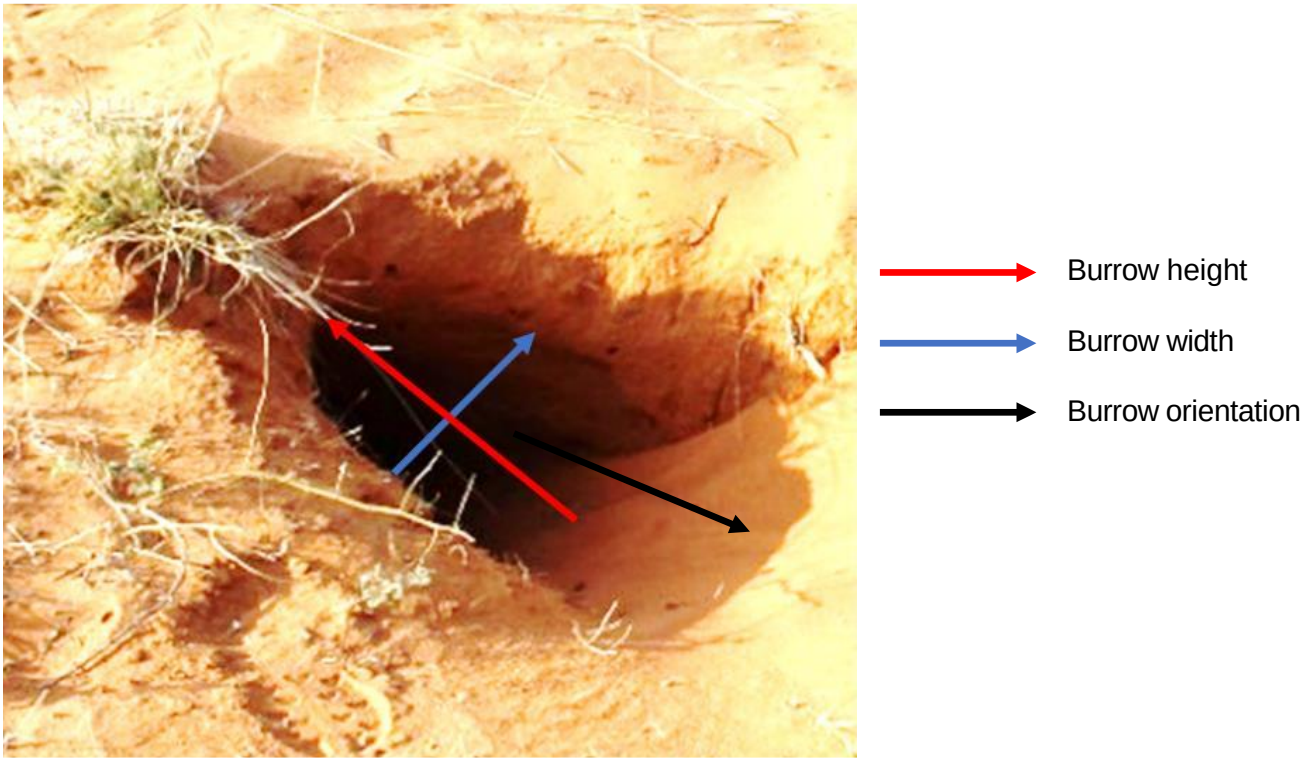

Figure 4.3: An aardvark (*Orycteropus afer*) /pangolin (*Smutsia temminckii*) burrow at Tswalu Kalahari Reserve, Northern Cape province, South Africa (Photo credit: Wendy Panaino).

The entrance of each burrow was swept clean by dragging a rake or broom around the burrow entrance. The width of the swept area was about 60 cm. The burrows were swept as early as possible during the day to reduce disturbance to any resident aardvark or pangolin, which would likely emerge in the afternoon or evening. The next day the observers returned to assess whether any fresh tracks exited the burrow, suggesting that an animal was inside the burrow the day before when the transect was surveyed.

Only burrows with tracks that exited the burrow were analysed, even though all burrows were recorded, to ensure that an animal was inside the burrow during the transects surveyed and that the animal did not emerge from one burrow and enter another within the

same transect, thereby reducing the probability of duplicating detections. On two occasions, observers were confident that the burrows were already occupied during the time when the transect was surveyed (before sweeping) through the presence of tracks likely from the night before. Therefore, camera traps (Cuddeback 20MP IR – Infrared flash H-1453, Camera Traps cc, South Africa) were placed outside those two burrows to ground-truth the detection of fresh tracks emerging from the burrows the next day. At one burrow, an individual aardvark emerged, and at the other burrow, a pangolin with a pup emerged. Since the pangolin pup was on the mother's back and thus did not leave any tracks of its own, pangolin detection may have been underestimated when pangolin pups were moved by the mother.

4.2.4 Burrow characteristics

For each burrow that was detected, I recorded burrow height and width (vertical and horizontal length of each burrow entrance) (Figure 4.3) using a measuring tape, and the orientation of the entrance using a GPS compass. I characterized the features around the burrow such as tracks, fresh soils, and a wide-open entrance to determine if the burrow was used by an aardvark or a pangolin.

I tagged four pangolins with Very High Frequency tracking transmitters (~40 g; 55 x 32 mm) during the study period. I monitored each pangolin to determine whether it showed a preference for a particular burrow orientation in winter. Each tagged pangolin was tracked three times per week during their inactive phase (when they were inside the burrow). At each burrow that the tagged pangolin occupied, the orientation of the burrow entrance, the side of the dune (east or west) that the burrow occupied if on a dune transect, GPS, height, and width of the burrow entrance were recorded.

4.2.5 Burrow temperature

Burrow temperature was recorded by placing a temperature data logger (DS1922L Thermochron Data Logger (-40 °C to 85 °C, accuracy 0.5 °C, Thermochron iButton, Dallas Semiconductor Products, USA) that recorded temperature every 30 minutes inside a randomly selected burrow. The burrow was unoccupied, was on a dune and had a west facing entrance. The data logger was attached to a 1 m long aluminium pole inserted level

with the roof of the burrow so that the data logger hung just inside the roof of the burrow and was not disturbed by any animal inside the burrow. The data logger was retrieved and downloaded using OneWireViewer downloader (DS9490R USB 1-Wire RJ11; DS9490B USB Single F5 iButton Holder, Dallas Maximum Products, China). The height of the burrow entrance and the width of the burrow entrance was measured using a measuring tape. A data logger was also placed in a black globe 1 m above the ground at Dedeben Research Centre (approximately 14 km away from the centre of the study site) to measure black globe temperature at 30-minute intervals. Experience at the reserve is that any weather station equipment is damaged by wildlife if it is left unattended in the open area of the reserve.

4.2.6 Grass cover

Details of grass cover scoring are given in section 2.2.4 Chapter 2.

4.3 Data analyses

Excel 2016, R, and Graphpad Prism (version 8.0.2) were used to prepare raw data for analysis and to create graphs. Burrow temperature was averaged hourly, daily, and monthly. A chi-square (χ^2) test was used to compare the number of burrows found on the dunes and dune streets, as well as to compare the number of east and west-facing burrows found on each side of the dunes. An unpaired *t*-test was used to compare the mean number of burrows detected on the northern and southern sections of the study area, as well as to compare the mean number of burrows recorded during transect surveys of the dune and dune street. The relationship between grass cover and the number of burrows recorded, and between time of day and burrow temperature, was analysed using Spearman's correlation. A paired *t*-test was used to assess the difference between black globe temperature and burrow temperature, and the relationship between black globe temperature and burrow temperature was assessed using Spearman's correlation. The data were first checked for normality using residual plots and presented as mean ± standard deviation.

4.4 Results

4.4.1 Burrow density

Over a total area of 7.625 km^2, 260 active burrows were detected. The average number of burrows per transect was 4 ± 6 SD (range = 0 to 31). The total number of burrows, as well as burrow density, was higher on the southern section of Tswalu Kalahari Reserve (200 burrows; 55 burrows/km^2) than on the northern section (60 burrows; 15 burrows/km^2) (t_{59} = 3.42; *n* = 260; *P* < 0.01). The southern section of the reserve had higher average grass cover (27 ± 12%) than the northern section (18 ± 14%) (t_{59} = 2.70; n = 45; *P* <0.01). The density of burrows was significantly correlated with grass cover (r = 0.55; *P* < 0.01) (Figures 4.4 and 4.5A). The number of burrows was significantly correlated with grass cover (r = 0.55; *P* < 0.01; Regression line equation: y = 0,1041*x + 1,178).

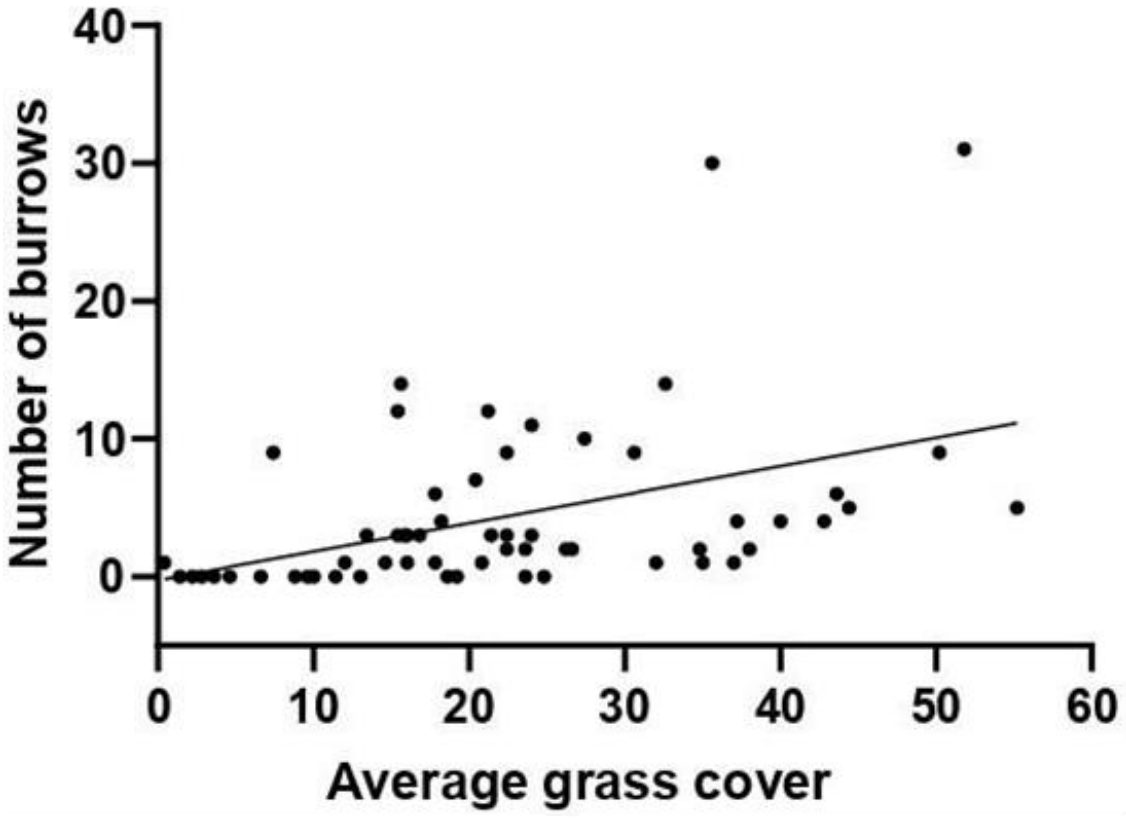

Figure 4.4: A linear regression between number of burrows of aardvark (*Orycteropus afer*) and pangolin (*Smutsia temminckii*) per transect and average grass cover on the transect. The number of burrows was significantly correlated with grass cover (r = 0.55; *P* < 0.01; y = 0,1041*x + 1,178).

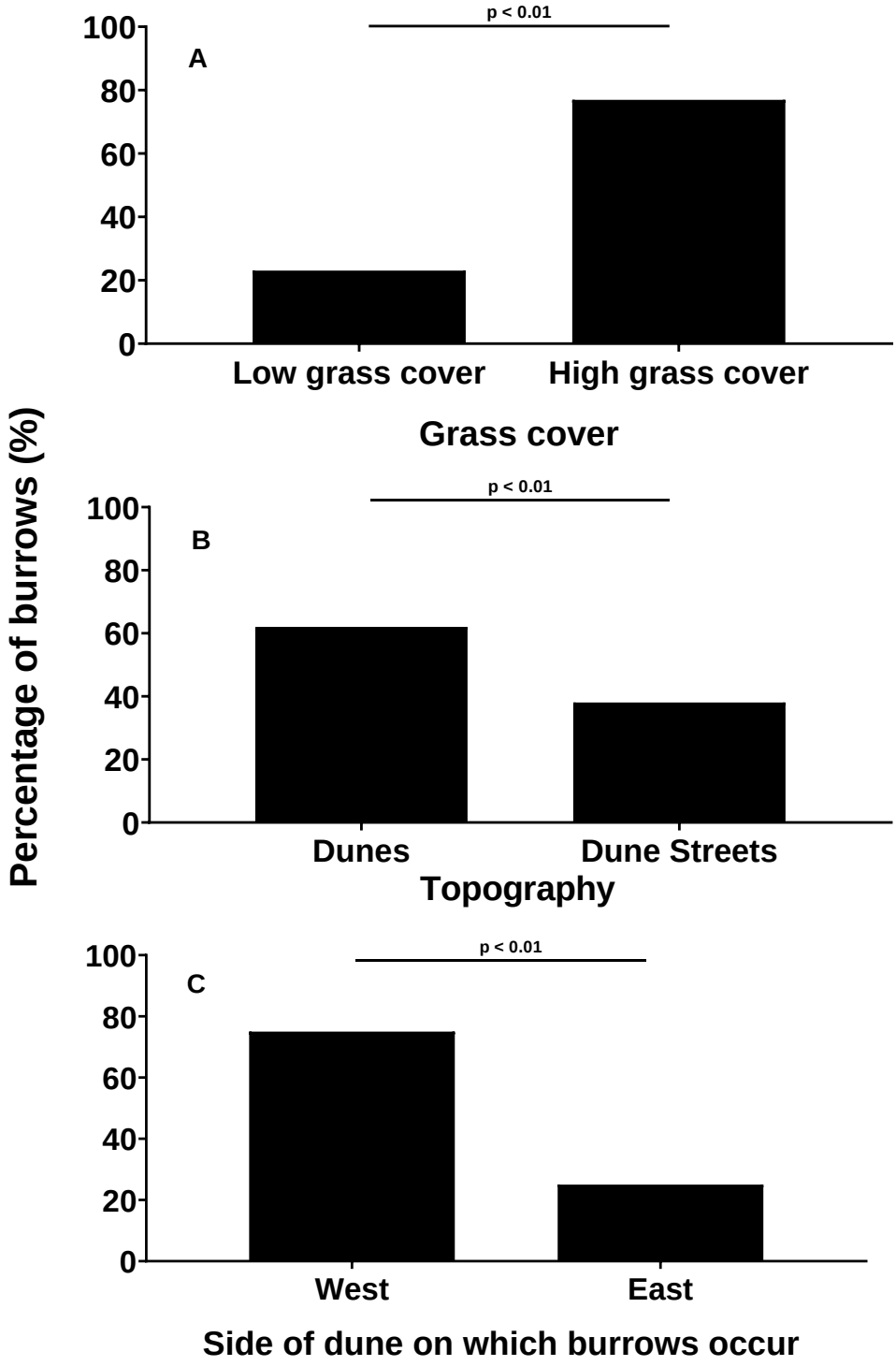

Figure 4.5: Percentage of burrows recorded in areas with A) low and high grass cover (*P* <0.01), B) in different topographical areas of the study area (*P* < 0.01), and C) on the western and eastern sides of surveyed dunes across the complete study area (*P* < 0.01) at Tswalu Kalahari Reserve, Northern Cape province, South Africa.

Most of the burrows (62%) were on the dune areas (160 burrows; 40 burrows/km^2) with fewer burrows (38%) on the dune streets (100 burrows; 28 burrows/km^2) ($\chi^2 = 14.7$; $n = 260$; $P < 0.01$) (Figure 4.5B). The pattern was similar in the two sections on the northern section of the study area where most of the burrows (80%) were on the dune areas (34 burrows; 16 burrows/km^2) with fewer burrows (20%) on the dune streets (9 burrows; 5 burrows/km^2) ($\chi^2 = 16.9$; $n = 43$; $P < 0.01$) (Figure 4.5B). In the southern section of the study area, most of the burrows (58%) were on the dunes (126 burrows; 66 burrows/km^2) with fewer burrows (40%) on the dune streets (91 burrows; 52 burrows/km^2) ($\chi^2 = 5.6$; $n = 217$; $P = 0.02$).

Of the burrows that occurred on dunes, the total percentage of burrows, as well as burrow density, was higher on the western side of the dunes (162 burrows; 60 burrows/km^2) than on the eastern side (55 burrows; 20 burrows/km^2) ($\chi^2 = 40.8$; $n = 217$; $P < 0.01$) (Figure 4.5C). Most of the burrows were on the western side of the dunes (75%) than on the eastern side of the dunes (25%) (Figure 4.5C). In the northern section of the study area, there were more burrows on the western side of the dunes (66%) than on the eastern side (34%), although the burrow density on the western side (23 burrows; 22 burrows/km2) and on the eastern side of the dunes (12 burrows; 11 burrows/km^2) did not differ ($\chi^2 = 3.5$; $n = 35$; $P = 0.06$). In the southern section of the study area, there were more burrows on the western side of the dunes (78%) than on the eastern side (22%). The burrow density on the western side of the dunes was higher (98; 102 burrows/km^2) than on the eastern side (28 burrows; 30 burrows/km2) ($\chi^2 = 38.9$; $n = 126$; $P < 0.01$). On the western side of the dunes, the west facing burrows were preferred (55%) while on the eastern side of the dunes, the east-facing burrows were preferred (30% of east facing burrows). In the dune streets, west-facing burrows (28%) were preferred (Figure 4.6A).

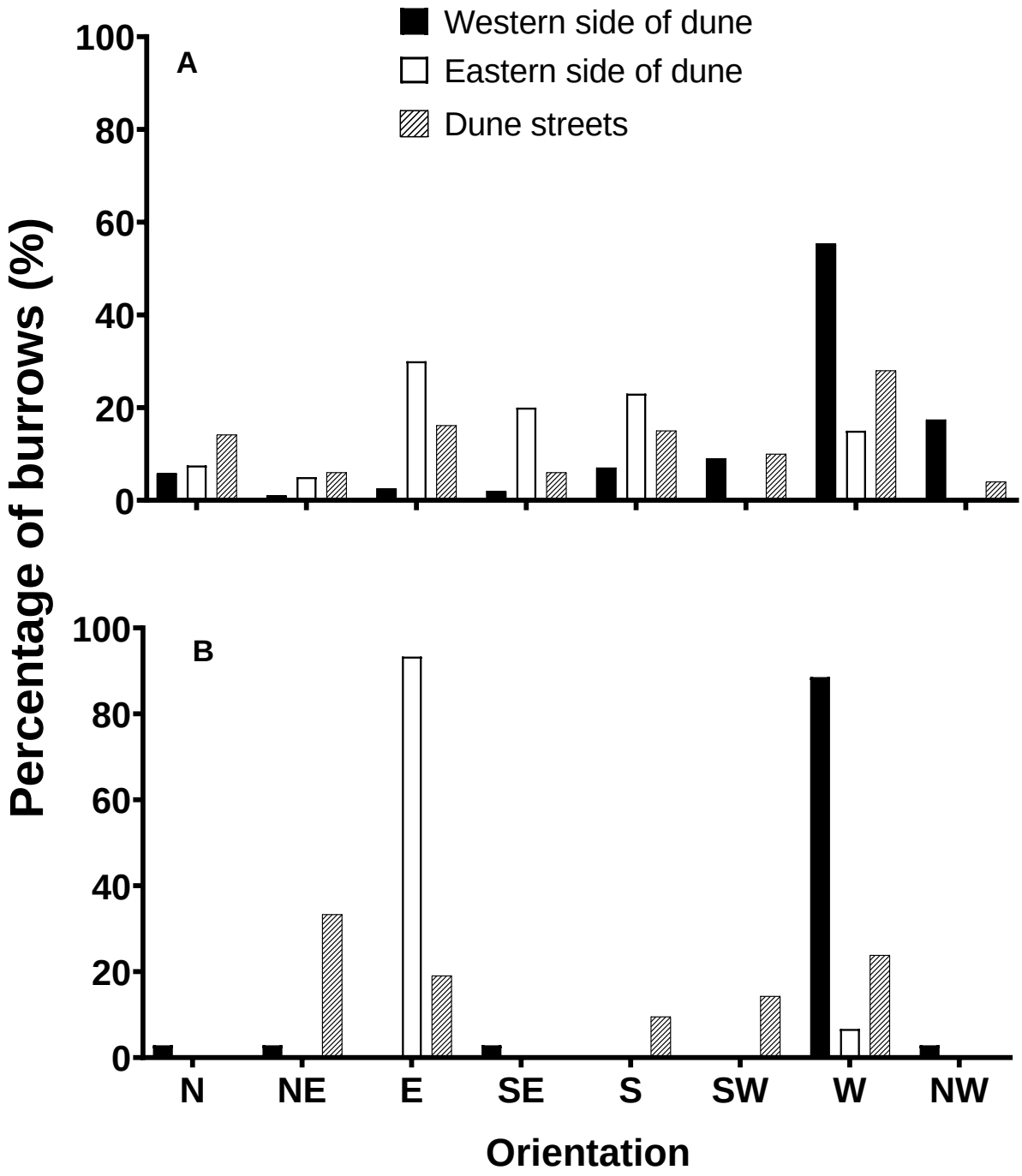

Figure 4.6 The orientation of the entrance of recorded burrows on different sides of surveyed dunes and on dune streets for northern and southern sections of the study area combined (A) and the orientation of the entrance of burrows used by tagged pangolins (*Smutsia temminckii*) in the southern section of the study area (B) at Tswalu Kalahari Reserve, Northern Cape province, South Africa.

4.4.2 Burrow usage by tagged pangolins

On the western side of the dunes, tagged pangolins preferred west facing burrows (88%), and on the eastern side they preferred east- facing burrows (93%) and in the dune streets tagged pangolins preferred northeast facing burrows (33%) (Figure 4.6B). Pangolins preferred burrows on the dune areas (70% of all burrows on dunes) than in the dune street areas (30%) ($\chi^2 = 11.5$; $n = 73$; $P < 0.01$) (Figure 4.7A) and preferred using burrows on the west side (70% of burrows on the west) of the dunes rather than burrows on the east side (30% of burrows on the east) ($\chi^2 = 8.6$; $n = 51$; $P < 0.01$) (Figure 4.7B).

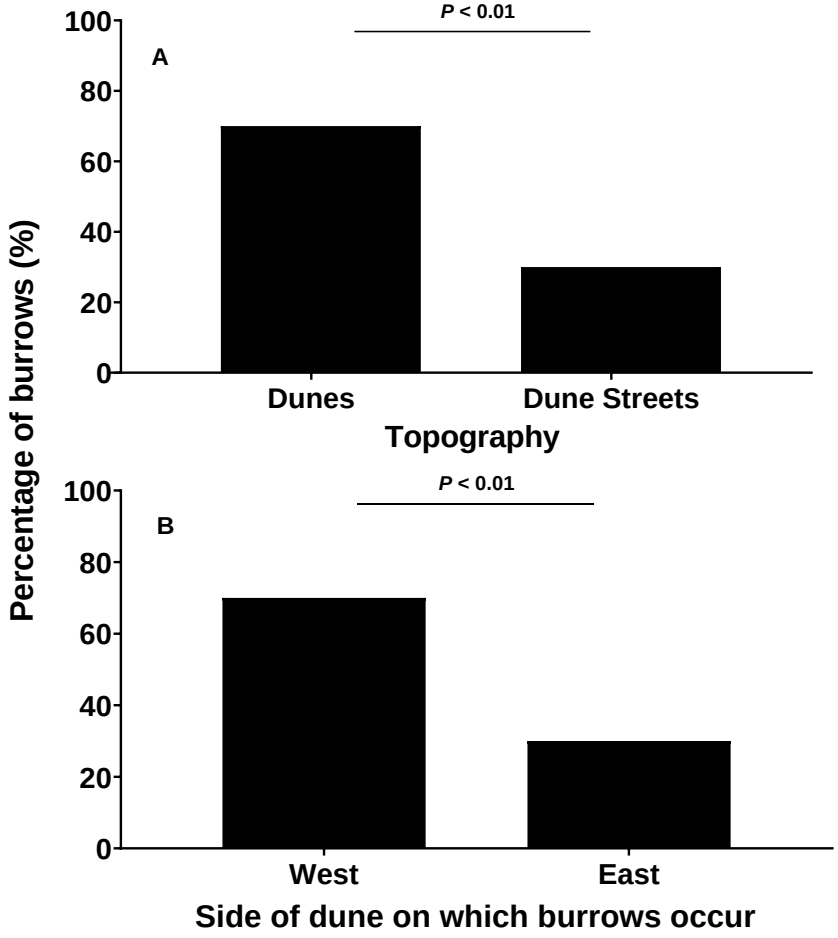

Figure 4.7 A) The percentage of total burrows occupied by tagged pangolins in different topographical areas in the southern section of the study area ($P < 0.01$) and B) the percentage of total burrows occupied by tagged pangolins on different sides of surveyed dunes in the southern section of the study area ($P < 0.01$) at Tswalu Kalahari Reserve, Northern Cape province, South Africa.

4.4.3 Burrow and black globe temperatures

The daily range of black globe temperature (Mean = 14.6 ± 12.0; range = 48.1) was higher and more variable than burrow temperature (Mean = 16.4 ± 5.5; range = 28.5) (t_{4210} = 11.53; $P < 0.01$) (Figures 4.8 and 4.9). Black globe temperature was significantly correlated with burrow temperature (r_{4210} = $P < 0.01$; Regression line equation: y = 0,2406*x + 12,91) (Figure 4.9) and increased more rapidly than burrow temperature in the mornings. Burrow temperature was significantly correlated with time of day (r_{23} = 0.65; $P < 0.01$) (Figure 4.10), with burrows beginning to warm up in the morning, reaching their warmest between 11h00 and 17h00 and cooling off in the evenings.

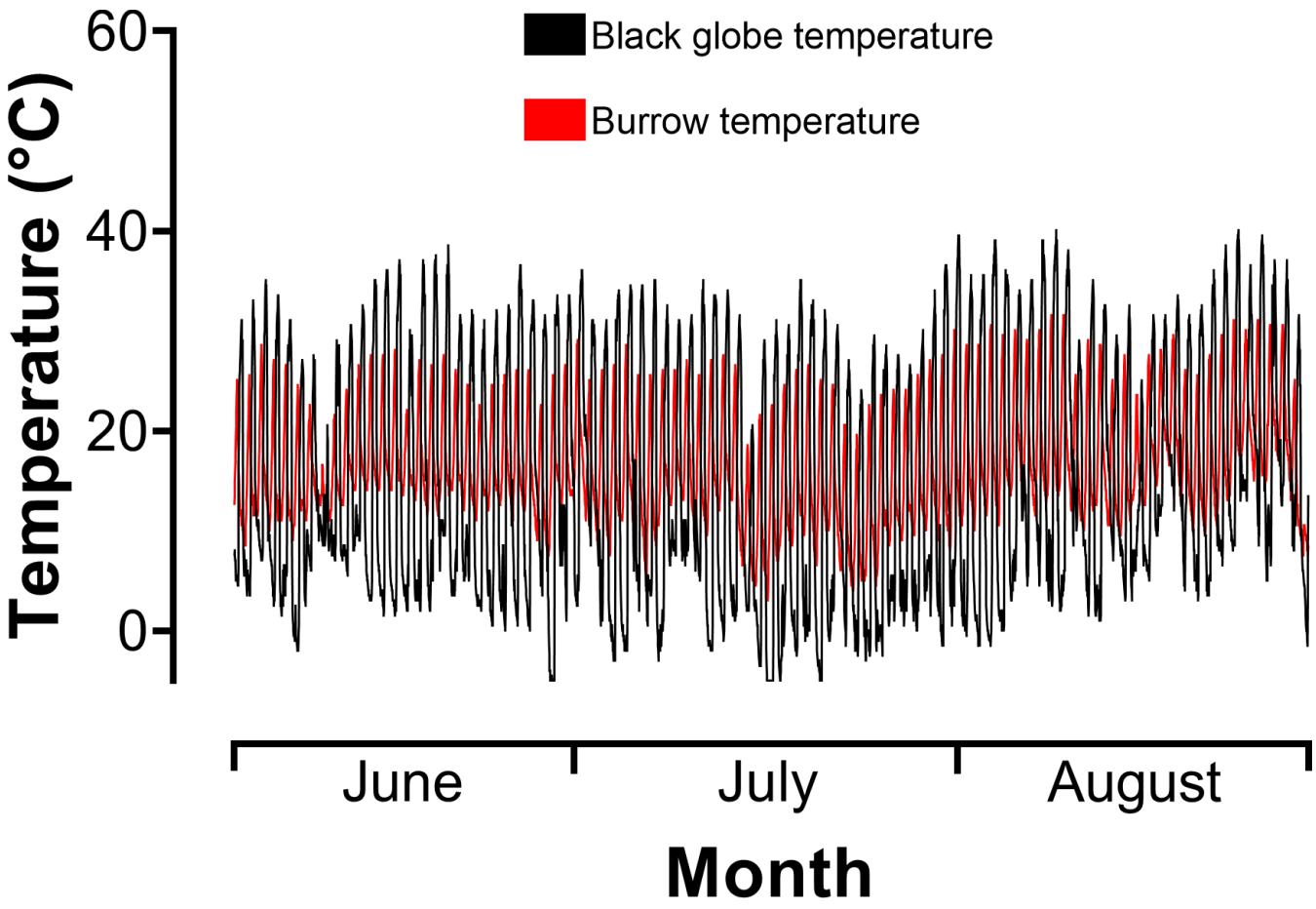

Figure 4.8: The daily range of black globe and burrow temperature during winter of 2021 at Tswalu Kalahari Reserve, Northern Cape province, South Africa. Black globe temperature was more variable than burrow temperature (t_{4210} = 11.53; $P < 0.01$).

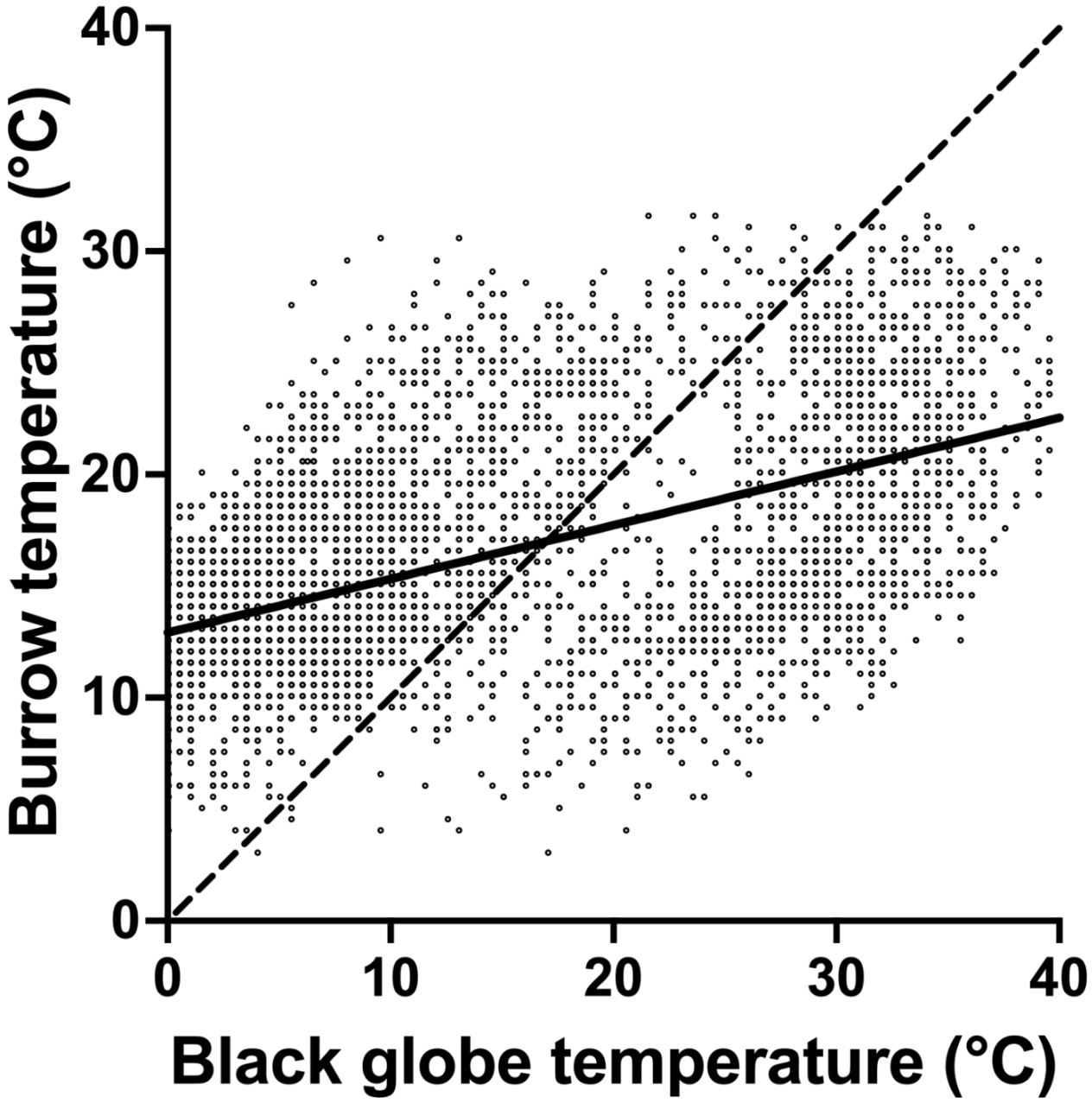

Figure 4.9: Relationship between black globe temperature and burrow temperature at Tswalu Kalahari Reserve, Northern Cape province, South Africa. The solidline shows the actual correlation between burrow and black globe temperatures and dotted line shows the line of identity. Black globe temperature was significantly correlated to burrow temperature (r_{4210} = 0.52; P < 0.01; y = 0,2406*x + 12,91), and the slope was significantly <1.

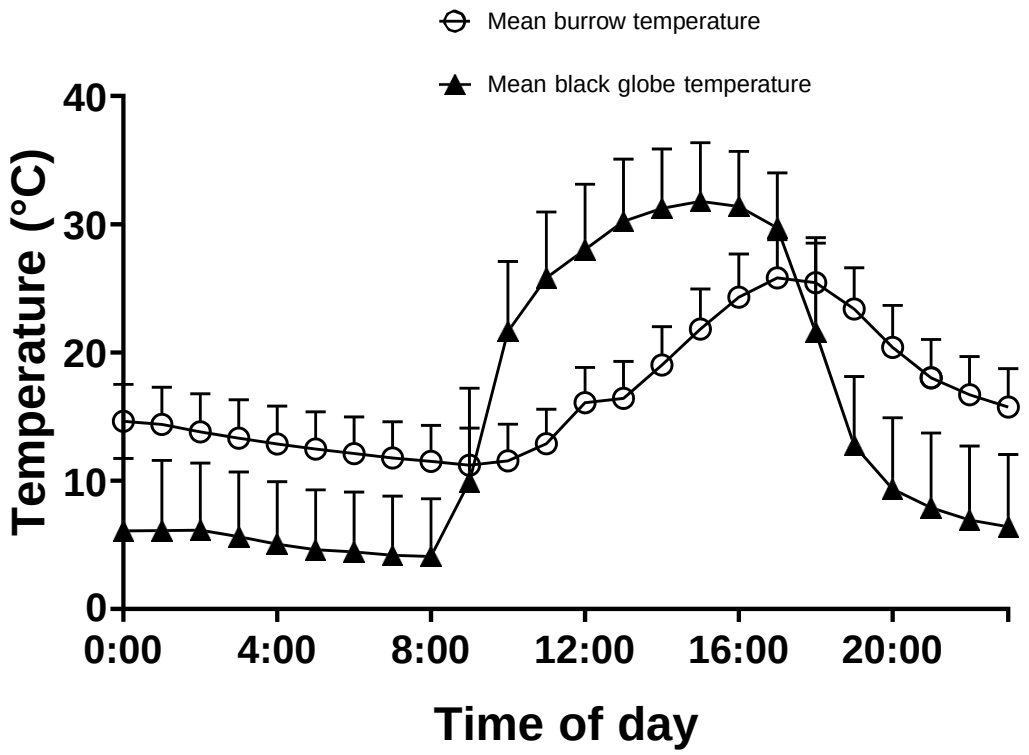

Figure 4.10: The mean ± SD of black globe and burrow temperature over 24-h during the three-month winter period at Tswalu Kalahari Reserve, Northern Cape province, South Africa.

4.5 Discussion

The present study showed that there was a positive association between the density of burrows and grass cover at Tswalu Kalahari Reserve, Northern Cape province, South Africa. The southern part of the study area, with higher grass cover, had 3-times more burrows (55 burrows/km^2) than the northern part (15 burrows/km^2). There were more burrows in the dunes (40 burrows/km^2) than in the dune street (28 burrows/km^2) area. There was a higher density (60 burrows/km^2) of active burrows on the western side of the dunes than on the eastern side. On the dune streets, more burrows were west facing. Burrows facing in all eight orientations (N, NE, E, SE, S, SW, W, NW) were available to aardvarks and pangolins, but there were more active burrows on the western side than the eastern side. Overall, the evidence suggests that burrowing animals at the study site had a preference for either excavating or using burrows on the western-facing slopes of the dunes. Tagged pangolins preferred burrows on the dunes compared to the dune street

areas. Tagged pangolins preferred west facing burrows on the western side of the dunes than the eastern side. Black globe temperature varied more with higher maximum and lower minimum temperatures than burrow temperatures. Burrow temperature was significantly affected by the time of day, as was black globe temperature which reached higher maximum temperatures earlier in the day than the burrow temperature because of the delay in how the temperature inside the burrow responded to changes in external conditions. The maximum temperature recorded in the burrow was considerably lower than the maximum black globe temperature. The west facing burrows began to warm in the morning, reaching their highest temperature between 14h00 and 17h00 pm, while black globe reached its highest temperature between 15h00 and 17h00 pm, and then decreased in the evenings.

My study assessed the density of burrows during winter, which may have resulted in some limitations in the interpretation of the data that I collected. Reduced activity can make it challenging to study the behaviour of aardvarks and pangolins. The detection of burrows is generally lower during winter than summer due to reduced burrowing activity during the colder months. However, this decrease in detection does not necessarily mean that the number of burrows decreases during winter. Many burrowing animals, such as the aardvark and pangolin, may use the same burrows year- round, the reduction in detection may be because they are less active during winter. There may be fewer insects available for the aardvark to feed on due to reduced insect activity during the cold and dry periods. During summer, the animals dig more burrows during winter because some burrows may collapse due to rainfall damage (Milling et al., 2018). Summer is when rainfall events occur that lead to vegetation and food abundance (Davies et al., 2015). Summer is the breeding season for most mammals and these species require shelter to raise their young (Qi et al., 2012; Taylor et al., 2016; Santamaria et al., 2019). The grass cover score was also low in the study area as it was recorded during the dry winter period. The present study also found more active west facing burrows possibly because it was during winter, and animals may have been targeted burrows that were warmer in the early evening. For example, the body temperature of pangolins in the Kalahari during summer is regulated between 34 and 36 ºC and is lower during winter (Panaino et al., 2023). A further limitation of the study was that burrow temperature was recorded in only one burrow, at one depth, and in one

location. The burrows counted in the present study ranged from 20 to 60 cm in diameter as smaller dimensions would likely be too small for the aardvark to use (Whittington et al., 2011; Legendre and Botha-Brink, 2018). Future studies should include a range of burrow sizes that the aardvark and pangolin can enter. Long-term monitoring, alongside indirect methods such as track surveys or burrow mapping, soil coring, and droppings should be incorporated, along with the use of camera traps to provide more valuable insights into the density of burrows.

Food, shelter, and water are critical elements for the survival of animals in all habitats, but particularly in drylands with extreme temperature fluctuations (Krebs, 1985; Taylor and Skinner, 2003). I found that grass cover was positively associated with the presence of burrows, such that animals using the associated burrows possibly had better access to food resources because of the presence of grasses and the insects that are associated with that grass cover (Whittington-Jones et al., 2011; Epps et al., 2021). Burrowing animals often excavate their burrows near food sources which is considered to reduce energy expenditure and the cost of foraging (Spinks et al., 2000; Heath and Vanderlip, 1988; Whittington- Jones, 2006; Pietersen et al., 2014; Martin, 2017). Behaviour is a strategic adaptation that allows burrowing animals to minimize the distance and effort required to access their food resources (van Aarde et al., 1992; Swart, 1996; Taylor and Skinner, 2004). An additional advantage is that burrowing animals can quickly return to their burrows after foraging and reduce the risk of predation (Ross et al., 2010; Tsunoda et al., 2018).

The distribution of the aardvark and pangolin is understood to be linked to the presence of ants and termites as their key prey species (Soewu and Sodeinde, 2015; Martin, 2017; Epps et al., 2021). Many ant and termite species depend on grasses (stems, seeds, and microorganisms) (Dean and Milton, 1993; Weyer, 2018; Parr and Bishop, 2022) as their primary food source (Kawahara et al., 2021; Panaino et al., 2022). The abundance of grass cover can serve as an indicator of the presence of ants and termites (Tscharntke and Greiler, 1995; Botes et al., 2006; Moll et al., 2012), supporting the insect populations and providing suitable shelter, and improving soil structure, preventing erosion, and increasing soil stability (Mizumoto and Matsuura, 2013). When ant and termite colonies decline, the

earth mounds can remain stable due to the protection provided by the grass cover that stabilizes and shelters the mound (Pullan, 1979; Erens et al., 2015).

Insects that rely on grass for shelter and protection from extreme temperatures may not be able to find suitable habitats under hot and dry conditions. Disruptions in insect populations and their interactions with plants can have a cascading effect on the broader ecosystem. Grass cover offers protection from extremely high environmental temperatures (Andrew et al., 2013), with insects reducing surface activity and remaining in their colonies at times when they do not forage because of extremely high temperatures (Panaino et al., 2022; Parr and Bishop, 2022). However, the presence of continuous grass cover can facilitate the movement and foraging activities of these insects, increasing their accessibility to resources and in turn their availability to predators (Roschard and Roces, 2003; Wills and Landis, 2018; Jimenez-Soto et al., 2019). For example, ants are ectothermic and cannot regulate their body temperature (Hazel, 1995; Willmer et al., 2000; Abram et al., 2017). Ants prefer temperatures within a certain range that falls between moderate and warm to hot temperatures within which to forage, although this may differ depending on the local thermal regime. In general, cool environments or during winter, the foraging activity of ants (i.e., number of foraging workers) is unimodal, and peaks at the warmest time of the day (Cros et al., 1997). In hot environments and seasons, a bimodal daily foraging schedule is seen where the extreme midday heat and relatively low temperatures during dawn and dusk are avoided (Greenaway, 1981). Consequently, as temperatures rise it is likely that many ant species will flexibly adjust their foraging schedules (Bernstein, 1979; Villalta et al., 2020).

Hotter and drier conditions can have a significant impact on grass cover, which in turn can affect the insects that depend on grass for survival. In the Kalahari, the presence of grasses is often associated with rainfall, as grasses are adapted to a wide range of environmental conditions and are particularly well-suited to areas with sufficient moisture. However, low rainfall in a region can result in dry conditions and less grass cover, leading to less prey abundance and/or availability (such as ants and termites) which can lead to drought stress over time (Gibb et al., 2019; Almeida et al., 2023). The cascading effects begin with reduced water availability for grasses (Orr and O'Reagain, 2011). In the Kalahari

(Weyer (2018) and Panaino et al. (2022) showed that decreased grass cover reduced the abundance of ants and termites, which impacts negatively on myrmecophagous mammals.

I counted 260 burrows over the survey area of 7.625 km^2, giving a density of 34.1 burrows/km^2. The density of burrows in the present study was higher than in a study conducted in the lowveld that surveyed 1,786 km^2 along the road and found 186 burrows with a density of 0.05 - 0.42 burrows/km^2 (Epps et al., 2021). The significant difference between the two studies might relate to the survey method used. Some animals will avoid digging burrows close to roads to avoid the roads and disturbances (Gibbs and Shriver, 2002; Barrientos and Bolonio, 2009; Roznik and Johnson, 2009; Nafus et al., 2013). Thus, the earlier study by Epps et al. (2021) probably underestimated the true density of burrows. The high vegetation density also might have affected the detection of burrows (Epps et al., 2021). A study conducted by Whittington-Jones et al. (2011) on the density of burrows in the Karoo and the Kalahari showed that burrow densities were 516 burrows/km^2 in Kwandwe Game Reserve, 795 burrows/km^2 in Mountain Zebra National Park) and 122 burrows/km^2 in Tswalu Kalahari Reserve. However, the methods used in the Kalahari (Whittington-Jones et al., 2011), the Lowveld (Epps et al., 2021) and Nama Karoo (Whittington-Jones et al., 2011) were slightly different from the present study. There is an indication that environmental conditions, including climate, vegetation, and sandy soils can influence the availability and characteristics of suitable burrows for burrowing mammals.

Sandy soils in the Kalahari have a loose structure and texture than the heavy or rocky soils to compacted or clay-rich soils that are found in other regions such as the Lowveld (van Rooyen et al., 1999). The characteristics of sandy soils can influence the ease of the burrow construction as they are more loosely packed, drier, and allow burrowing animals to dig through them easily and more efficiently (Butynski and Mattingly, 1979; Shenbrot et al., 2002; Wu et al., 2015). Sandy soils tend to retain less moisture than heavy compacted soils (Seymour et al., 1998). However, adaptations such as specialized claws, powerful digging muscles, or behavioural strategies (Swart, 1996; Pietersen, 2013; Weyer, 2018; Panaino, 2021) can help animals overcome the difficulties posed by different soil types while digging for burrows that may require more energy for the animal to dig (Downs and Perrin, 1989; Weyer, 2018; Gul and Griffen, 2019).

There is an energetic cost to creating a new burrow (Vleck, 1981; Hildner and Soule, 2004; Gul and Griffen, 2019) and in sandy soils that cost it is generally lower than it is in other soil types, reducing the energy expenditure required for burrow construction (Vleck, 1979; Wu et al., 2015). Given the relationship between soil type and energy expenditure, it is necessary to carefully consider and optimize the location of a dig. Factors such as soil and vegetation characteristics, and prey distribution must all be considered to maximize the efficiency and effectiveness of burrow construction (Reichman and Seabloom, 2002; Kinlaw, 2006). The cost includes the physical exertion and metabolic energy that is required for digging, shaping, and reinforcing the burrow structure. Studies on digging by other burrowing animals (Reichman and Seabloom, 2002; James et al., 2009; Wu et al., 2015) and the aardvark (Skinner and Chimimba, 2005) has reported that digging in soft and deep plain soils and low basal vegetation cover, allows for lower energy expenditure (Vleck, 1979) than the construction of burrows in areas with denser soil. Diggings of aardvark burrows have also been reported to occur more during the rainy season when the soil is soft than during the dry season (Makwati, 2022). In the present study, the burrows occurred at a high density in soft and deep soils, as similarly reported in previous studies (Watkeys, 1999; Mucina and Rutherford, 2006; Whittington-Jones, 2006).

Burrows in the Kalahari were more commonly found on dunes than on dune streets. In agreement with other studies (Whittington-Jones et al., 2011; Weyer, 2018, Panaino, 2021; Tamang et al., 2022), burrows on the dunes are likely to be more stable, with narrower tunnels than on flat terrain. The narrower tunnels in aardvark burrows also provide support to the surrounding soil, reducing the risk of collapse. (Dentzien-Dias and Figueiredo, 2015). The burrow can also have multiple entrances connected by short lateral tunnels (Kingdon et al., 2013), and the aardvark may use these multiple entrances to easily enter and exit (Melton, 1976; Taylor and Skinner, 2003; Taylor and Skinner, 2004).

In the case of the pangolin, the higher prevalence of pangolin burrows on dunes than dune streets may also have been influenced by various factors such as the combination of soil characteristics, vegetation dynamics (Bulova, 2002; Louw et al., 2019), stability (Wu et al., 2004), and microclimatic conditions (Whittington-Jones et al., 2011) which makes the dunes in the Kalahari a more favourable habitat for burrowing animals. The higher grass

cover on dunes than dune streets can significantly influence the soil chemistry through processes such as nutrient cycling. The apparent paradox is solved because of what the vegetation does to the soil chemistry leading to higher organic matter input, increased microbial activity, and greater nutrient cycling in the dune areas. Dunes offer more stable substrates and are completely stabilized by vegetation (Ashkenazy et al., 2012; Thomas and Wiggs, 2022) than the dune streets in terms of burrow construction. The accumulation of sand and the shaping of dunes by wind creates a relatively more consolidated and structured environment, which is appropriate for burrow stability (Downs and Perrin, 1989, Woolnough and Steele, 2001; Ashkenazy et al., 2012).

The presence of grass cover and its associated prey abundance on the dunes than the flats terrain can attract burrowing animals, leading to a higher density of burrows in those areas. Forty seven percent of burrows of the Chinese pangolin (*Manis pentadactyla*) were found on steeper slopes with suitable foraging sites (Tamang et al., 2022). The selection of burrow sites by the Chinese pangolin was found to be positively correlated with elevation and the availability of prey resources (Tamang et al., 2022). Similar results to the present study were also found in a study on a reptile, the gopher tortoise (*Gopherus polyphemus*) in northeastern Florida in the United States of America where there was a greater abundance of burrows used by the tortoises on higher elevation dunes and crest areas than elsewhere (Blonder et al., 2021).

I found a higher density of burrows on the western side of the dunes than on the eastern side, with more burrows having a west facing orientation. A burrow on the western side receives more direct sunlight and warmth in the afternoon when the sun is at its peak, creating a warmer microclimate inside the burrow as the day progresses into the early night (Singh, 2018). The finding highlights the importance of considering environmental factors such as sunlight exposure and orientation when studying burrowing behaviour and habitat preferences in dune ecosystems. By understanding the impact of these factors on burrow microclimates, researchers can gain valuable insights into the adaptive strategies that are employed by burrowing species to survive in challenging environments.

The orientation of a burrow can also create a natural windbreak and reduce the risk of sand accumulation inside the burrow. The prevailing wind in the Kalahari is from the east and so a burrow facing west or southwest is less likely to be exposed to windblown sand into the entrance of the burrow. Animals can reduce the risk of sand accumulation inside their burrows presumably because the prevailing winds are from the east. It has been reported that the entrances of aardwolf burrows are at ground level with little direct exposure to the prevailing wind and therefore unlikely that wind was affecting the orientation of burrows used by the aardwolf (Anderson and Richardson, 2005). The use of an existing slope for burrowing and the orientation of the burrow could potentially influence the thermal microclimate of a burrow if the entrance faces in the direction of the greatest thermal input (McCoy et al., 1993; Wood, 1997). However, the temperature inside a burrow can be influenced by other factors including the size of burrow entrance, depth and orientation of the burrow, soil type, and moisture content (Kirmiz, 1962; Finlayson et al., 2005; Martin, 2017). The use of slopes for burrowing and the orientation of the entrance to aardvark and pangolin burrows has not received much attention in the literature and therefore these aspects of burrow ecology require further investigations.

The direction in which the entrance of the burrow faces may influence the time of the day that the burrow cools and warms (Dean and Williams, 2004; Ke and Lu, 2009; Whittington-Jones et al., 2011). The orientation of the burrow entrance determines how it interacts with solar radiation and the prevailing wind, affecting the temperature dynamics within the burrow (Nagy and Medica, 1986; Diemer, 1992; Milling et al., 2018). My study found more west facing burrows than other orientations and thus I placed a temperature logger inside a west facing burrow. Burrows with west facing entrances receive more direct sunlight into the burrow during the afternoon than those burrows facing other directions (Frost et al., 1976). Burrows used by the Chinese pangolin were found mostly in the directions that are warmer (Northwest) than other orientations which makes the environment appropriate for their survival during the cold winter months (Dorji, 2017). According to Wu et al. (2004), the openings of burrows of pangolins often face west where they are exposed to sunlight for a longer duration, which can contribute to increased heating and the maintenance of higher temperatures inside the burrow during winter.

The direction in which the entrance of the aardvark and pangolin burrows face can influence the timing of cooling and warming in the burrow (Weyer, 2018; Panaino, 2021). In the Kalahari during winter, aardvarks tend to emerge early either in the morning or late in the afternoon to forage, and then they retreat to their burrows when the outside temperature drops below ~2 °C (Taylor, 1998; Taylor and Skinner, 2003). When aardvarks and pangolins emerge in the afternoon, they may initially experience a warmer environment due to the direct sunlight, which can be important for their thermoregulation. The daily temperature fluctuations inside the west facing burrow in the present study were between 3 and 10 °C and were broadly similar to the study by Whittington-Jones et al. (2011) where temperature fluctuations were between 6 and 10 °C. Burrow temperatures recorded in the present study were higher than the temperatures recorded in the burrow of springhare and aardwolf that were less than 5 °C (Peinke and Brown, 2003; Anderson and Richardson, 2005). The entrance of the burrow in my study was 20 × 20 cm, while the entrance of springhare burrow is smaller, averaging 13.2 × 16.8 cm (Anderson and Richardson, 2005).

In conclusion, burrows serve as a beneficial buffer against climatic conditions for burrowing species. The density of burrows is positively associated with grass cover. More burrows were found on the southern section of Tswalu Kalahari Reserve with more grass cover than the northern section of the reserve that had less grass cover. More burrows were found on dunes than on dune streets, predominantly on the western sides, offering heat avoidance during the day and providing warmth during the night. Tagged pangolins preferred west facing burrows on the dunes over the flat terrain. Burrow temperature was significantly affected by the time of day. The west facing burrow was cooler in the morning and warmer in the afternoon towards sunset. Although finding in this study contribute to an understanding of the burrow densities associated with grass cover, it was limited to winter. The burrow with the temperature logger faced west and future investigations should focus on assessing burrow temperatures in other burrow orientations and in all seasons. The absence of aardvarks can lead to trophic cascade effects, highlighting the interconnectedness of species and the importance of keystone species in maintaining ecological balance.

Chapter 5- Social media as a tool to understand the ecology of two elusive mammals: the aardvark and ground pangolin in Southern Africa

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Abstract

Comparatively little is known about the distribution and ecology of aardvark and Temminck's ground pangolin. Both are elusive species that are normally nocturnal, solitary, and fossorial. Formally collected records have been used to map the distribution of these species, and social media records provide a tool to gather information on their distribution and ecology. I collected 680 photographs and videos of aardvarks and 790 of ground pangolins in southern Africa from publicly available posts on Facebook and Instagram (2010 – 2019). The images provide new insights into the distribution, activity, drinking, and predation, and confirm that aardvarks are more diurnally active when they are in poor body condition. Social media can provide useful supplementary information for understanding elusive mammals. This 'soft' data can be applied to other species.

Keywords: distribution, activity pattern, biodiversity, body condition, southern Africa

5.1 Introduction

The conservation of mammals in the face of threats such as illegal trade, habitat loss, and climate change requires the regular collection of data on the abundance and distribution of those animals, as well as the factors influencing their ecology. Direct monitoring of most mammals is costly and labour-intensive, so proxy methods such as camera trapping, transects for animal signs, and molecular techniques such as environmental DNA metabarcoding have instead been used. Even with those proxy methods, elusive species are particularly difficult to monitor, often resulting in major knowledge gaps. The aardvark and Temminck's ground pangolin are two such species. They are challenging to detect as they are primarily nocturnal, solitary, occur at low densities, and are fossorial (Ingram et al., 2019; Epps et al., 2021).

The ground pangolin is listed as vulnerable on the IUCN Red List of Threatened Species (IUCN, 2019; Pietersen et al., 2019) and is threatened primarily by illegal trade and harvesting (Challender et al., 2015; Tenorio and Baril, 2019), habitat destruction, road mortalities, and electrocution by electrified fences (Beck, 2008; Pietersen et al., 2014b). More recently, climate change, through its effect on ant and termite availability, has been identified as an additional threat (Panaino et al., 2022). The indirect impact of climate change on termite availability has also been identified as a threat to the aardvark (Rey et al., 2017; Weyer et al., 2020), despite the species currently being classified as of Least Concern (Taylor and Lehmann, 2015; Taylor et al., 2016).

Aardvarks and ground pangolins perform key roles in their ecosystem as predators of social insects and as creators of burrows. As predators of ants and termites, they contribute to the control of insect populations (Chao et al., 2020). Through their digging of burrows, they impact soil processes, including turnover of soil organic matter, acting as bioturbators that expose underground insects to other predators (Taylor, 2013; Irshad et al., 2015; Chao et al., 2020), and provide burrows that are used by other species that are incapable of digging burrows themselves (Whittington-Jones et al., 2011). Given the knowledge gaps for both species, increasing threats to their survival, and their ecological importance, it is important to improve monitoring.

One way to supplement the efforts of researchers is through citizen science (Chandler et al., 2017). A citizen science platform such as iNaturalist provides millions of digitally verified biological sightings (Di Cecco et al., 2021) but has few high-quality records for aardvarks and pangolins. Another less formal platform for species observations, which may provide additional data from a broader base of observers, is social media. A recent survey of geotagged posts of Twitter and Flickr for the word “pangolin” confirmed the presence of pangolins within the IUCN geographic ranges (Di Minin and Hausmann 2020), while Instagram posts with the identifiers #monkseal provided information on Hawaiian monk seal (*Neomonachus schauinslandi*) (Sullivan et al., 2019). Social media has also been used to elucidate ecological processes, as shown through a recent study using Facebook records of trophic interactions for southern African herpetofauna as predators and as prey (Maritz and Maritz, 2020).

I hypothesized that publicly available social media records would provide information on the distribution and ecology of aardvarks and ground pangolins. I searched posts on Facebook and Instagram for photographs and videos of aardvarks and ground pangolins in southern Africa, and summarized the distribution of records, as well as other information on the species’ ecology.

5.2 Materials and methods

5.2.1 Data collection

I searched publicly available posts from 2010 to 2019 on Facebook and Instagram for photographs or videos of aardvarks and ground pangolins. Search terms used (Appendix Figure A7) included the scientific and common species names used in southern Africa. We collected posts with clear (species definitely identified) images or videos of aardvarks or pangolins, including those from camera traps. Posts were manually filtered to remove images where animals were captive or reintroduced into the wild or poached. Images where animals appeared to have died of natural predation were included. Searches were restricted to southern African countries namely South Africa, Namibia, Botswana, Zambia, Zimbabwe, Malawi Mozambique, Angola, Lesotho, and Eswatini. No records were found for Angola, Lesotho, or Eswatini.

5.2.2 Data capture and processing

Data from posts on aardvark and ground pangolin were captured in a spreadsheet. The source of the photograph included (Facebook or Instagram), the date of the posting, and the location where the photograph was taken (country, province/region, and place within the province/region). Duplicates were removed where the same animal appeared to have been photographed by more than one person at a similar time, or posted more than once by the same person, or posted on both Facebook and Instagram. The date of the posting was used to code the images as occurring in spring (September to November), summer (December to February), autumn (March to May), or winter (June to August). Each photograph was inspected, and the time of day coded as: daytime (not specified), morning, afternoon, or night-time (18h00-06h00). Where time of day was not indicated on the post, light intensity, the use of a spotlight, and whether camera trap images are grey scale (infrared, after dark) or colour (daytime) of the animal were used to code day or night (transitional periods where I could not be sure of the cut-off were classified as night). Camera trap images typically provided exact time detail. Animals were classified as to whether they appeared alive or dead, and if dead, whether a predator was captured in the image. Whether an animal appeared to be drinking also was recorded.

5.2.3 Body condition assessment

The body condition of aardvarks was assessed using a visual appearance scale ranging from 1 = ‘emaciated’ to 4 = ‘fat’ (adapted from Russel 1991; Thompson and Meyer 1994; Weyer 2018). Two reviewers (LCRM, NMW), experienced in working with aardvarks, scored the images independently. Where there was disagreement between the two reviewers, a third reviewer (MVP) arbitrated. Of the aardvark images, 481 of 680 were suitable for rating body condition. The body condition of ground pangolins cannot be assessed visually as the animals are covered by scales.

5.3 Data analyses

Analyses were conducted using R (v4.2.0; R Core Team 2022), with the ggplot2 package (Wickham, 2016) used to generate plots. The number of posts of aardvarks and ground pangolins were counted for each country. For South Africa (the country that accounted for most posts), the data were separated by province. For southern Africa, the annual and

seasonal patterns of sightings (stratified by time of day), and the number of drinking and predation (stratified by predator) events were summarized. Based on feedback from the body condition reviewers, before analysing the relationship between body condition and the time of day that the sighting took place (daytime or night-time), the body condition data were collapsed into two groups: poor condition (condition scores of 1 or 2), and good condition (condition scores of 3 or 4). These data were then analysed using logistic regression with time of day (daytime vs night-time) as the outcome measure.

5.4 Results

After cleaning the data, I had 680 photos and videos of aardvarks and 794 of ground pangolins. South Africa had more than 80% of each (Table 5.1). Further analysis of the posts from South Africa revealed that aardvarks were seen in all provinces, with most of the sightings in the Northern Cape (34%), followed by Limpopo (19%) and the Eastern Cape (18%) (Figure 5.1). Ground pangolin posts were in four provinces only, Northern Cape (50%), Mpumalanga (34%), Limpopo (14%) and North West (2%) (Figure 5.1). Aardvark (146) and pangolin (316) sightings were most common at Tswalu Kalahari Reserve in the Northern Cape, followed by Kruger National Park (98 aardvark, 289 pangolin) (Figure 5.1). Data collected for South Africa revealed that aardvarks and ground pangolins were seen in all seasons.

Across the whole of southern Africa, most aardvark posts were from observations in winter (47%), followed by spring (22%), autumn (17%) and summer (14%). Pangolin posts were also most common in winter (38%), followed by spring (27%), autumn (19%) and summer (16%). About half (53%) of all the observations of aardvarks were during the day, for pangolins, 26% of all posts were in the day. Assessment of the time of sighting by season revealed that aardvarks were seen mainly in the night, except in winter when most sightings were in the afternoon (Figure 5.1). In contrast, there were no clear differences with season in the times of pangolin observations. (Figure 5.1). There were no clear long-term patterns in the time of day for aardvark or pangolin observations. Aardvarks were seen most at night in 2014 (excludes 2010 when there was only one post made), while pangolin observations were rarely seen at night in 2012.

Table 5.1: Source of aardvark (*Orycteropus afer*) and Temminck's pangolin (*Smutsia temminckii*) images by country.

Country	Aardvark Count (%)	Ground pangolin Count (%)
South Africa	571 (84)	673 (85)
Namibia	46 (5)	31 (4)
Botswana	23 (3)	34 (4)
Zambia	23 (3)	19 (2)
Zimbabwe	8 (1)	5 (1)
Malawi	5 (1)	19 (2)
Mozambique	4 (1)	13 (2)
Total	680	794

From the 481 images and videos that were suitable for rating aardvark body condition, 306 aardvarks (64%) were in "good condition". Just over half (268) were captured when it was daytime. There was a strong association between time of day and body condition, such that an animal in poor body condition was more likely to be observed during the day [Odds ratio (95% CI): 0.08 (0.05; 0.13), z = -9.63, P-value < 0.001] (Figure 5.2).

There were 32 records of aardvarks drinking water across all months except December (Figure 5.3). There were seven posts of ground pangolins drinking, mostly in the warmer months (Figure 5.3). Predation was observed at almost all times of the year for both species. Aardvarks and ground pangolins were preyed on by spotted hyena, leopard, and lions, with leopards being the most common predator for aardvarks (84%), and lions the most common predator for ground pangolins (79%, Figure 5.3).

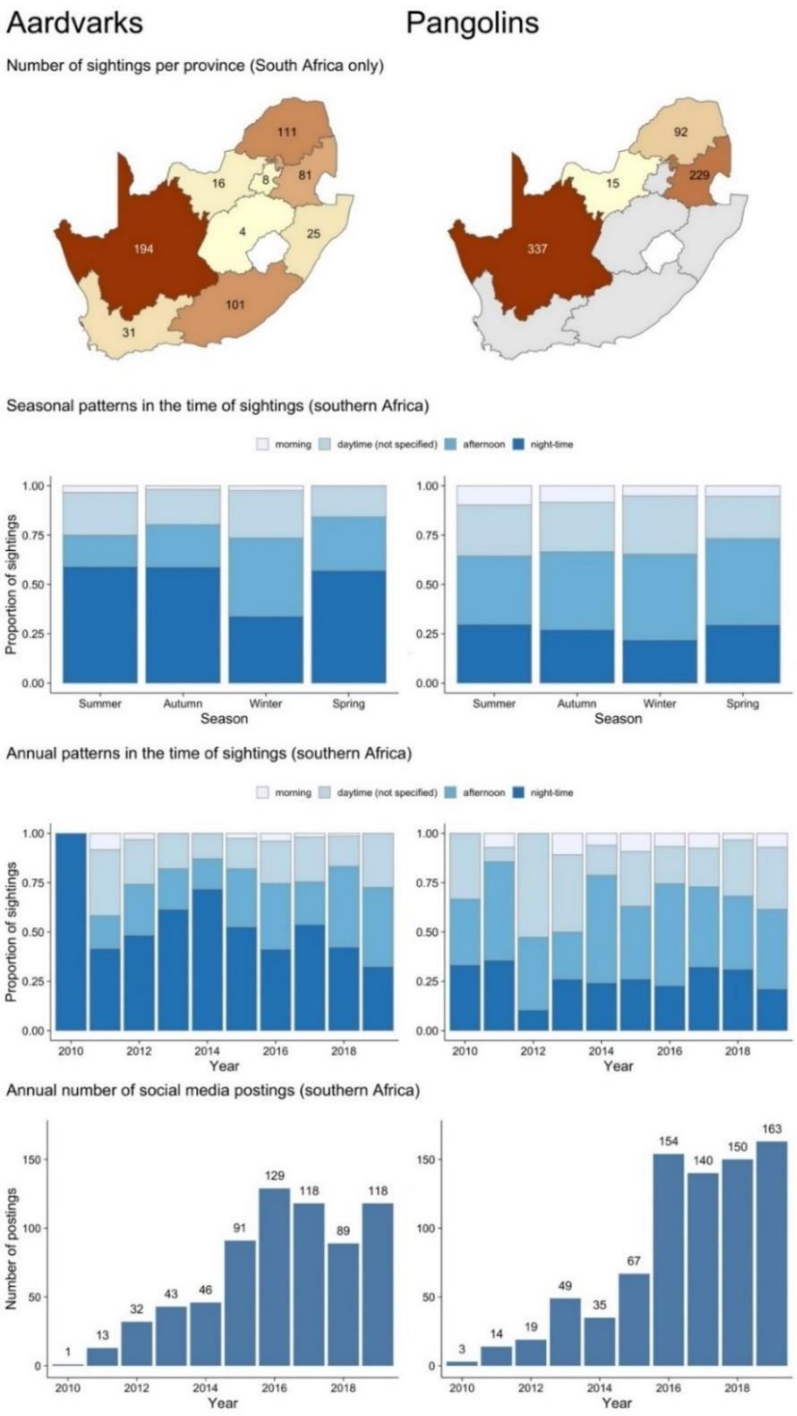

Figure 5.1: The number of distinct posts of aardvarks (*Orycteropus afer*) (left) and ground pangolins (*Smutsia temminckii*) (right)in South Africa, and the seasonal and annual patterns in the time of sightings, as well asthe number of postings, from southern Africa over a ten-year period, from 2010 to 2019 using Facebook and Instagram social media images.

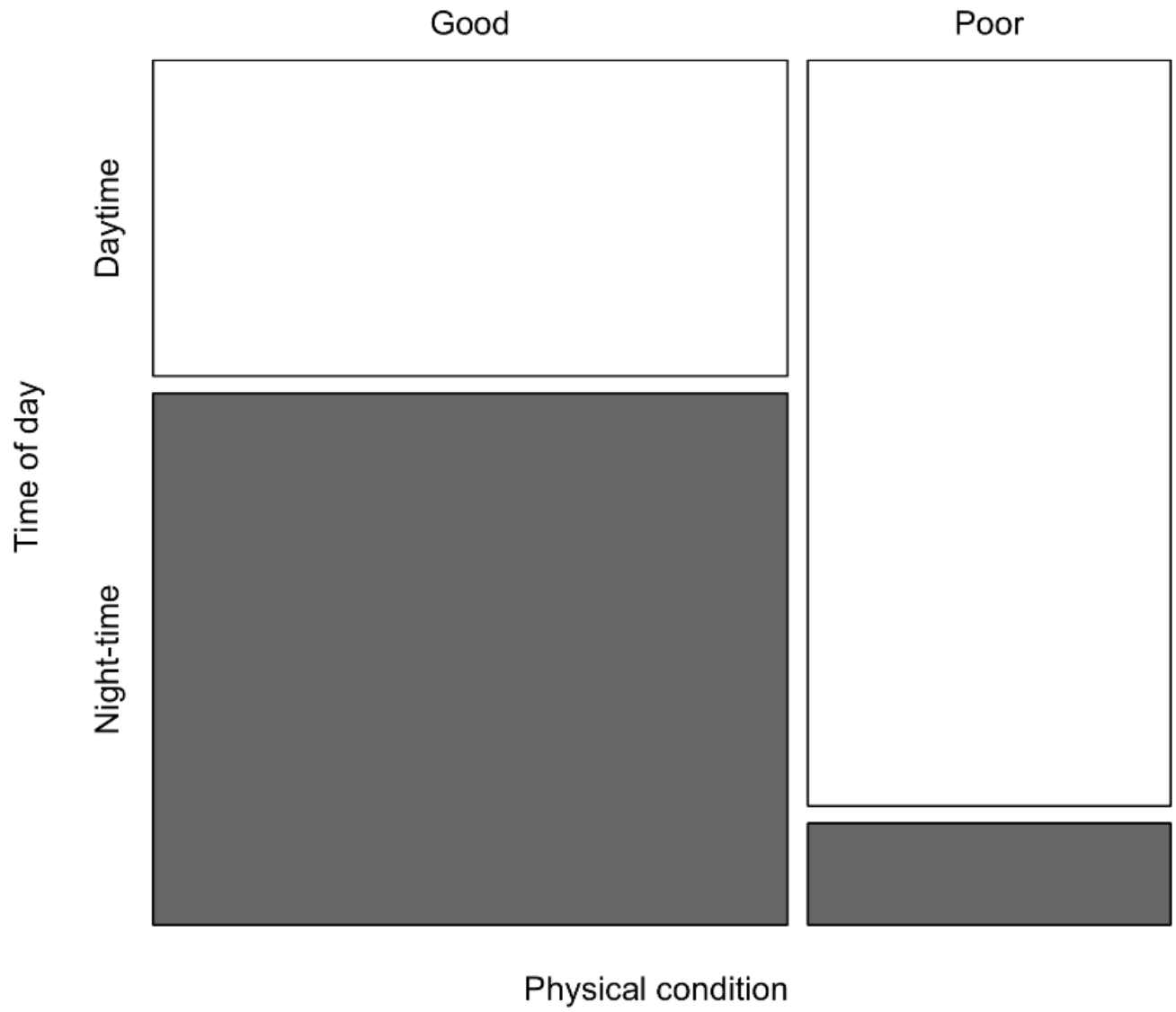

Figure 5.2: The relationship between aardvark (*Orycteropus afer*) body condition and the time of day. There was a strong association between the time of day and body condition of the observed animal, such that aardvarks in poor body condition were seen more often in daylight, whilethose in good body condition were observed more often at night.

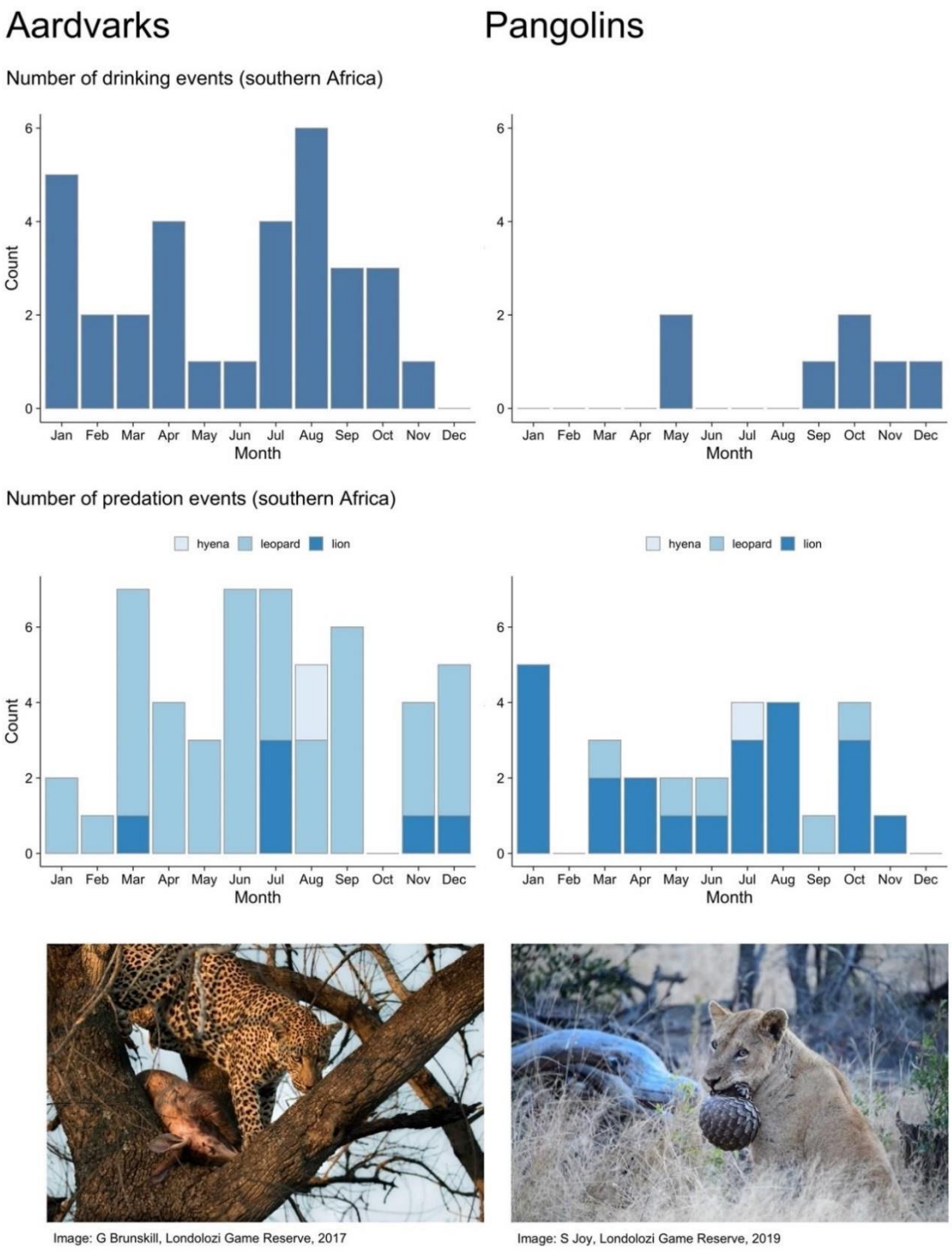

Figure 5.3: The number of drinking and predation events of aardvarks (*Orycteropus afer*) (left) and ground pangolins (*Smutsia temminckii*) (right), and example images of predation by a leopard on an aardvark, and a lion on a ground pangolin, from Londolozi Game Reserve in South Africa.

5.5 Discussion

Social media provides supplementary information on two elusive mammals. The images of aardvarks (*n* = 571) and ground pangolins (*n* = 673) in South Africa confirm that aardvarks are found throughout South Africa while ground pangolins are restricted to the northern regions. There were far fewer records for other southern African countries, making it difficult to draw conclusions about distribution in those areas. In terms of the time of day of observations, ground pangolins were more commonly seen in the daytime than at night-time across all seasons. In comparison, aardvarks were more likely to be seen at night, except in winter when daytime observations were more common. Changes in the time of observations over 24-h across different years are difficult to compare because of an increase in the number of observations posted on social media for both species, particularly from 2010 to 2016. However, changes in the relative number of observations at night and in the day between years may reflect changing environmental conditions, given that aardvarks in poor body condition were seen more often in daylight, whereas those in good condition were seen more often at night. Social media provide records of rarely observed drinking and predation for aardvarks and ground pangolins, and in the dataset, leopards are the main predator for aardvarks, while lions are the main predator for ground pangolins.

The major potential limitation in drawing inferences from the dataset is that it is influenced by human behaviour. An area such as the Kalahari is known to be favourable for observing ground pangolins and aardvarks, so increased ecotourism to that area for those sightings may bias the distribution counts. Similarly, the activity patterns of guests will influence the time of observations, across seasons and the 24-h day. For example, at Tswalu Kalahari Reserve, where many observations of both species were collected (Figure 5.1), guests are more likely to undertake early morning (04h30 – 09h00) and late afternoon (17h30 – 22h00) game drives in the hot summer, and day game drives (06h30 – 17h00) in the cooler winter with only occasional night drives (Prince Ngomane, Tswalu Kalahari Reserve, personal communication). Changing patterns across years are also difficult to interpret because the number of social media users, and therefore the likelihood of posted social media observations, has been increasing in recent years. I did find an increasing number of posts over time, with a relatively low number of posts from 2010 to 2015.

For example, the number of users of the popular Facebook page “Kruger Sightings” continued to increase across the 10-year data collection period. Tourist seasonality and the size of the tourism industry also would need to be considered when using social media records to draw inferences from seasonal or annual changes in species numbers, distributions, or activity. Camera trap images of aardvarks, which comprised 22% of the total records that we found on social media, can provide continuous monitoring across the day and year, but require significant investment to cover the same regions as those explored by tourists, as well as image processing to identify species.

Despite the potential biases introduced by changing tourist and social media activity, the records I gathered confirm the known distributions for aardvarks and ground pangolins and provide a substantial increase in the number of records available for each species (Taylor et al., 2016; Pietersen et al., 2021). Most records of aardvarks and ground pangolins are largely confined to protected areas and their distribution is determined by the availability and suitability of ant and termite species, and soil that is conducive to digging burrows (Pietersen et al., 2016; Taylor et al., 2016). The findings confirm previous reports that ground pangolins do not extend to the southern part of the country and are likely to be locally extinct in the Free State, where the last record was in 1985 (Lynch, 1975, 1983). It is thought that overexploitation and habitat loss have reduced populations in the Free State, Eastern Cape, and KwaZulu Natal (Pietersen et al., 2014; Pietersen et al., 2020). Historically, however, ground pangolins have been found in KwaZulu-Natal and they are currently being reintroduced into the province (Pietersen et al., 2014; Murray 2015).

Social media data on Flickr and Twitter have been used before to draw inferences about the distribution of pangolins (Di Minin and Hausmann, 2020). Geotagged posts confirmed the presence of pangolins in 41 out of 54 countries in Africa and Asia, within the known IUCN geographic ranges. Facebook, the social media network with the most active users worldwide and the most popular for nature-related posts (Di Minin et al., 2015), has also been used to quantify media activity and public interest in pangolins and the pangolin trade (Harrington et al., 2018). One concern with accessing geotagged posts of pangolins is the risk of disclosing their location to potential poachers (Di Minin and Hausmann, 2020).

While distribution records based on social media posts may be biased by tourist behaviour and camera trap placement, data extracted from social media can outperform other citizen science image-based approaches, such as iNaturalist and Google images (Maritz and Maritz, 2020), and traditional data collection (Sullivan et al., 2019). At the time of writing, iNaturalist had 298 records for aardvarks and 38 for ground pangolins from southern Africa, far fewer than my sample. Some records provide only indirect evidence of aardvarks and pangolins (for example, an aardvark burrow, image observed June 2016, Benfontein Nature Reserve), and some of those are incorrect (tracks incorrectly labelled as being ground pangolin tracks, image observe December 2014, Sofala Mozambique). Inspection of those records also reveals errors (for example, an image of a Leopard tortoise (*Stigmochelys pardalis*) is labelled as an aardvark (image observed June 2016, Benfontein Nature Reserve). Camera trap images, likely offer better insights into phenology, and can reveal unusual animal behaviour (Pardo et al. 2021), without the potential disturbance by human observers.

In terms of activity patterns, I expected that aardvarks and ground pangolins would be observed more often at night than in the day, as both species are nocturnal (Taylor and Skinner, 2003). Aardvarks were seen more often at night, except in winter (Figure 5.1). Diurnal activity has previously been shown to be more common for aardvarks in winter than in other seasons (Taylor and Skinner 2003; Rey et al. 2017; Weyer et al. 2020) and appears to be a response to lower ant and termite availability rather than avoidance of cold (Weyer et al., 2020). Indeed, aardvarks in the Kalahari that were in poor body condition basked in the sun in the morning outside burrows, presumably to increase their body temperature through an exogenous energy source (Weyer, 2018). I hypothesized that aardvarks in poor body condition would be more likely to be seen in daylight, while those in good condition would be seen more often at night, and my data was consistent with that hypothesis (Figure 5.2). Aardvarks that were in poor body condition succumbed to apparent starvation in drought periods and may be threatened by increasing drying associated with climate change (Rey et al., 2017; Weyer et al., 2020), the continued monitoring of the timing of aardvark sightings may provide a useful tool for detecting the potential threat of climate change to aardvark survival.

Aardvarks and pangolins feed predominantly on ants and termites (du Toit et al., 2014; Pietersen et al., 2016; Chao et al., 2020) and are more likely to emerge from their burrows earlier in the day in the face of reduced food availability (Panaino, 2021). I did not detect a seasonal change in the pattern of timing of activity through social media images of ground pangolins, and only about a quarter of the images were taken at night, across all seasons (Figure 5.1). A likely explanation for my unexpected finding of more diurnal observations may be the difficulty of observing pangolins at night, given their much smaller size relative to aardvarks.

In addition to food energy, aardvarks and ground pangolins are thought to receive their water requirements mainly from their prey (Taylor and Skinner, 2004; Pietersen et al. 2016; Taylor et al. 2016). Ground pangolins are reported to rarely drink free-standing water (Pietersen, 2013; Challender et al., 2019; Panaino, 2021) and only seven records of aardvarks drinking water for the Karoo have been documented (Taylor and Skinner 2004; Skinner and Chimimba, 2005; Kerley and Tompkins, 2017). One advantage of mining social media data is insights into rare behaviour, such as drinking. I collected what I believe is the largest published dataset of drinking for aardvarks (n = 32) and ground pangolins (n = 7) (Figure 5.3). It is possible that both species may become more reliant on drinking water when they face higher heat loads in summer. Drinking may also occur more often when food is scarce (and hence there is reduced water intake through food) (Weyer 2018). Kerley and Tompkins (2017) published three images of aardvarks drinking, and all aardvarks in those images would be scored as being in poor condition using the scoring system. Of the 32 drinking images that I collected for aardvarks, 25 were suitable for body condition scoring, with 44% of those aardvarks rated as being in poor condition (overall 36% of the aardvarks assessed in my study were in poor condition). Ongoing collection of images revealing drinking episodes, particularly through camera traps placed at waterholes, would be useful in elucidating the importance of free- standing water in the ecophysiology of myrmecophagous mammals.

In addition to drinking behaviour, my image collection also provides insights on the predation of aardvarks and ground pangolins. I collected evidence of predation events in almost all months, with no clear seasonal patterns (Figure 5.3). Previous studies have

recorded African lions, leopards, hyenas, and honey badgers (*Mellivora capensis*) as predators of pangolins, although scales protecting pangolins make them difficult to penetrate and kill (Swart, 2013; Chao et al., 2020; Pietersen et al., 2020). Leopard, lion, spotted hyena, cheetah, wild dog and python (*Python natalensis*) have been observed preying on aardvarks (Bothma and Riche, 1984; Kingdon, 1997; Radloff and du Toit, 2004; Hayward et al., 2006; Williams et al., 2018). Aardvarks have been identified as one of the preferred prey items for lions in South Africa (Eloff ,1973; Power, 2002; Roxburgh, 2010). However, a systematic literature survey of the lion's diet across the lion's distribution range, with data on prey availability, revealed only one study with aardvark recorded as a potential prey item, with no available data for pangolins (Hayward et al., 2005). A similar analysis for leopards revealed three studies documenting aardvark as a potential prey item, and only one documenting pangolin (Hayward et al., 2006). From the images collected, leopards appear to be the main predator (84%) for aardvarks, while pangolins appear to be targeted mostly by lions (79% of predation images). It could be argued that the behaviour of leopards in hanging their prey in trees increases the likelihood that aardvark predation by leopards would be more readily observed, relative to that for lions. However, in most regions of southern Africa, it is much more likely that lions are observed by tourists than leopards are observed by tourists (Maciejewski and Kerley, 2014; Grünewald et al., 2016). The finding that the lion appears to be the main predator for pangolins is similar to previous studies (Chao et al., 2020; Petersen et al., 2020).

Further data on predation or drinking behaviour for myrmecophagous mammals, or indeed any other behaviours or interactions of interest, could be solicited through the targeted sourcing of images (for example, Maritz and Maritz, 2020). That initiative provided more than 1,900 independent feeding observations posted on Facebook, involving 83 families of predators and 129 families of prey. Relative to a literature review spanning 226 sources and 138 years, the authors found that social media provided dietary records for snakes at greater speed and a finer taxonomic resolution and revealed novel interactions (Maritz and Maritz, 2020).

In summary, the extraction of social media images reveals the potential to gather supplementary and novel information on the distribution and ecology of elusive species,

such as the aardvark and ground pangolin. Social media can be used to monitor the occurrence of species in various locations, but whether it can be useful in tracking changing population numbers over time, and therefore assist with conservation efforts, may be dependent on the number of social media users, and the number of posts, plateauing. The increase in the number of sightings of aardvarks and ground pangolins from 2010 to 2019 in the dataset likely reflects increasing numbers of Facebook and Instagram users in the country (Worldwide Worx, 2016; Statista, 2020). More people in South Africa use social media as compared to other southern African countries (Worldwide Worx 2016; Budree et al., 2019; Statista, 2020), so social media data may be less useful in countries with lower user numbers, or countries that are less attractive as tourist destinations. Nevertheless, particularly as automated methods are available to extract data from social media, I believe that it can be a useful tool for gathering information on data-deficient species.

Chapter 6 – Conclusions

Animals, or organisms in general, face a multitude of threats globally, primarily due to anthropogenic activities. Human-induced threats include poaching, encompassing illegal wildlife trade and over hunting (Soewu and Sodeinde, 2015; Challender et al., 2019; Makwati et al., 2023), and changes in land use driven by mining, agriculture, industrialisation, and urbanisation (Tilman et al., 2017). Changes in land-use, especially urban expansion, often induces habitat fragmentation (Wu et al., 2004; Katuwal et al., 2017; Sharma et al., 2020). Invasive species, introduced by human actions, further contribute to the challenges faced by many animals (Maxwell et al., 2016). Pollution, whether from industrial discharge or waste disposal, represents a pervasive threat to various species (Maxwell et al., 2016). Electrocution on fences and road mortalities are direct outcomes of the development of human infrastructure and expansion, resulting in additional risks (Pietersen et al., 2016; Pietersen, 2022; Stracquadanio et al., 2024). Uncontrolled bush fires, often induced by human activities, add to the list of anthropogenic threats faced by animals (Jolly et al., 2022). Rapid temperature change, rising sea levels, and extreme weather patterns resulting from climate change add to the list of threats by impacting negatively on ecosystems and habitats, driving many species to extinction. In addition, changes in rainfall and seasonal variability alter the availability of food and the movement patterns of animals, contributing to their vulnerability (IPCC, 2023; Schlaepfer and Lawler, 2023). To conserve these species, it is essential to understand the impacts of the threats on their survival, including their sensitivity and responses, and to monitor changes in their abundance and distribution.

According to the IUCN Red List, approximately 25% of known mammal species that were extant in the year 1500 have gone extinct due to human activities, together with 13% of all known bird species, and more than 21,000 other plant and animal species (IUCN, 2016). One of the most well-known examples is the iconic passenger pigeon (*Ectopistes migratorius*), which was once the most abundant bird species in North America (Schorger, 1973; Fulton et al., 2012). Due to hunting and deforestation, the passenger pigeon went extinct in 1914 (Schorger, 1973; Halliday, 1980; Fulton et al., 2012). Similarly, the extinction of the dodo (*Raphus cucullatus*) in the 17th century due to hunting and habitat destruction serves as a reminder of the impact of human actions on wildlife (Angst et al., 2017; Sakurai and Sakurai, 2019; Cheke and Perish, 2020). The extinction of marine

mammals, for example the Steller's sea cow (*Hydrodamalis gigas*) in the 18th century, highlights the devastating impact of human exploitation (Turvey and Risley, 2006). The Steller's sea cow, once found in the North Pacific, was hunted to extinction after its discovery by European explorers (Jones, 2014; Estes et al., 2016). Contrary to the belief that it was abundant, evidence indicates the species was already near extinction, with only a few isolated populations remaining (Stejneger, 1887; Berta, 2008). A Russian whaler crew reported sighting a small group off the Siberian coast in the Bering Sea, suggesting the species may have survived into the 19th century (Stejneger, 1887). Modeling extinction dynamics and hunting records from 18th century Russian expeditions, alongside data from the related dugong, show the species was vulnerable before European settlers arrived (Turvey and Risley, 2006; Sharko et al., 2021). Overfishing, pollution, and habitat destruction continue to threaten marine species today, with rapid declines in many populations of whales, dolphins, and seals. In addition to the well-studied larger species, the bleaching of coral reefs due to rising sea temperatures, for example, is causing mass die-offs of coral species and the loss of biodiversity in marine environments (Brierley and Kingsford, 2009; Marques and Marques, 2020; Warm and Lotze, 2021).

There is an estimated 69% risk of extinction for South African mammals by 2050 due to changing environmental conditions resulting from climate change, especially if their ability to disperse is restricted. As a result, iconic areas such as Kruger National Park in South Africa may be at risk of losing two-thirds of existing species (Thomas et al., 2004; Erasmus et al., 2002). These models, however, likely overestimate the impacts of climate change as they do not include the capacity of species to adapt through phenotypic plasticity (Hetem et al., 2014). Nevertheless, the extensive expansion of agriculture in sub-Saharan Africa, beginning with deforestation, also shows a strong and positive correlation with an increased risk of extinction for endemic species (Perrings and Halkos, 2015). Sheep ranching in Africa and Arabia has led to competition with wild herbivores, leading to reduced primary productivity and habitat degradation, particularly during periods of scarcity such as severe droughts (Keesing and Young, 2014). Human-induced changes in land use have profound effects on the distribution of wildlife and their prey, contributing significantly to a loss of global biodiversity (Ripple et al., 2015; Tilman et al., 2017).

The research focused on two elusive mammals that both inhabit arid regions. There is limited information available on how climate change is affecting their survival. Climate change can affect animals directly through increased exposure to higher temperatures or indirectly through effects on food or other resources. The aardvark and Temminck's pangolin are particularly vulnerable to the effects of climate change due to their unique habitat requirements and reliance on specialised food sources (Rey et al., 2017; Weyer et al., 2020; Panaino et al., 2022). For example, physiological studies in aardvarks raised concerns about how climate change affects performance due to limited availability of food sources (Rey et al., 2017; Weyer et al., 2020). In addition, habitat changes due to climate change, such as changes in vegetation cover and water availability, may affect the quality of habitat for aardvarks and pangolins. These species have specialised habitats, including access to burrows and good feeding sites, which may be affected by changes in ecosystems due to climate change. To understand how climate change is impacting on the species under study they must be monitored, but so must other organisms at lower trophic levels. Lack of water may directly affect insect activity/survival due to their osmotic needs, or indirectly via reduced soil moisture and its impact on the growth of grass, indirectly affecting insects that rely on grass for habitat and food.

There is a need to assess the resilience of aardvarks and pangolins to environmental change and anthropogenic stressors, analyse their responses to those changes, and predict potential changes in population and distribution. For example, it is important to learn how to manage ecosystem changes caused by urbanisation, deforestation, and climate change. Understanding the behaviour of aardvark and pangolin in response to environmental disruptions can provide insights into their adaptive mechanisms and challenges and research findings can help to develop targeted initiatives to mitigate threats. Understanding population dynamics and distribution patterns can help establish protected areas, conservation corridors, and habitat restoration strategies.

The Kalahari region is known for its hot and dry environments characterised by high temperatures and low precipitation, making it a challenging environment for many species, including ants and termites. Ants and termites are usually low in the Kalahari, but in my research, it was found that ants and termites responded differently due to the sudden

increase in rainfall and grass cover that was associated with a La Niña event. The unexpected behaviour suggests that these insects can adapt to changing environmental conditions, highlighting their resilience and adaptability in the face of adversity across trophic levels. Changes in one trophic level can have cascading effects throughout the ecosystem.

Because of the cascading effects throughout an ecosystem, a study on species across trophic levels can provide a better understanding of the complex relationships in ecosystems and the impact of environmental changes than a study on a single organism. By observing the responses of ants and termites to high rainfall in the Kalahari, a better understanding of how species are influenced by factors such as food availability, habitat preferences, and vulnerability to external stressors can be developed. An example is myrmecophagous mammals. Declines in ant and termite populations due to climate change may affect those mammals, because they rely on the ants and termites as food and a reduction in prey abundance will affect the survival and reproduction rates of those mammals. I therefore surveyed the abundance of ants and termites in the ecosystem, and at the same time used analysis of faecal samples to determine the composition of aardvark and pangolin diet and whether there was dietary overlap between the two mammalian species when resources were either abundant or scarce. The investigation was the first time that the diet of these two mammals had been assessed at the same time. Thus, the outcome enhances our understanding of their competition for prey availability.

There was some dietary overlap between the diets of aardvarks and pangolins throughout the study. The varying degree of dietary overlap between the two mammalian species appeared to be associated with primary productivity (rainfall). When rainfall was high in autumn, and hence when food was abundant, the dietary overlap was high, and when rainfall was low during spring, and food was scarce, the dietary overlap was low. In general, more food resources tend to lead to increased dietary overlap, as the species could presumably afford to be less selective, while limited resources drove the species to specialise and thus reduce competition (Chesson, 2000). Although the diets of the aardvark and pangolin overlapped across some of their preferred prey items, their predominant prey items differed. The aardvark fed predominantly on *Trinervitermes*

termites while the pangolin fed predominantly on *Crematogaster* ants. Because each species specialised on a different prey item, the limited interspecific competition between these two myrmecophagous mammals allows them to survive and coexist in their current environment. Both the aardvark and pangolin preyed on *Anoplolepis* ants and *Hodotermes* termites in addition to or as an alternative to their preferred prey items.

One limitation of the dietary overlap analyses in the present study was that it was conducted only over one year, and that year was an unusually wet year. Whether less competition occurs between the species in drier years remains to be determined, although the results suggest that the species would specialise even more in drier years, which would limit competition. It has been predicted that competition may increase between aardvarks and pangolins during droughts (Panaino et al., 2022; Weyer, 2018) but the studies were conducted in different years, limiting the applicability of direct comparisons. In addition, existing studies have examined the dietary overlap among several other myrmecophagous mammals in southern Africa, including the aardvark, aardwolf, bat-eared fox, Meller's mongoose, and Temminck's pangolin (Pietersen and Robertson, 2023). However, the extent to which aardvarks and pangolins directly compete for resources in areas where they co-occur remains unclear. It would also be useful to study other myrmecophagous mammals at the same time, such as the aardwolf and bat-eared fox at the same study site, and to compare their diets with those of the aardvark and Temminck’s pangolin. Investigating these features may lead to a better understanding of the competitive dynamics. Future studies should monitor competition between aardvarks and pangolins when food is scarce in the Kalahari drylands. Furthermore, investigating food patterns in sympatric and allopatric locations may indicate how each species adjusts its feeding behaviour in the presence or absence of the other, shedding light on the nature of their interactions.

Although the diets of the animals in the present study were assessed simultaneously, there are other myrmecophagous mammals in the ecosystem that could impact on the outcomes of competition. There are also other species that feed on ants and termites as part of a more generalist diet. To better understand the competition for ant and termite resources, the diets of several key species in the ecosystem would need to be assessed. In addition,

long-term studies should be conducted to understand long-term patterns and ecological changes. Long-term studies provide a more comprehensive view of the dynamics of resource competition, allowing researchers to understand patterns, assess the importance of seasonal variation, and understand the adaptive strategies of related species. Short-term deviations from trends are not as informative as long-term trends. Long-term studies can provide information to assess the impacts of management activities (Magurran et al., 2010, Dodds et al., 2012), provide context for other ecological studies (Lindenmayer and Likens, 2010), and monitor trends in biological indicators that serve as early-warning systems for declining ecological integrity (Magurran et al., 2010). The diet of myrmecophagous species may shift over time, and by studying the diets of multiple myrmecophagous species simultaneously and in the same environment, can improve our understanding of how these animals compete for resources.

Long-term data on prey abundance in regions sensitive to climate change is lacking and is essential to provide important insights into ecological responses to climate change over time (Tokura et al., 2018). For example, there are few long-term data records of insect abundance, especially in Africa. There is a need for long-term data on prey abundance for species that depend on insects for survival, such as the animals investigated in the present study, to understand changes over time and make better predictions on their future survival. The 8-year long-term insect data in the present study showed an overall decreasing trend in ant and termite numbers. Although the ants bounced back after the recent rainfall in 2021, the termites did not, as reflected by low numbers in the pitfall traps. While there are limitations in using pitfall traps to assess termite counts, low numbers of termites, compared to previous years, could indicate that termites are in a precarious position. Whether their populations have decreased substantially, and whether they will recover, if so, requires a long-term investigation. Termites build underground nests, many of which are made to withstand flooding; they may seek higher and drier areas within the nest to prevent their colonies from becoming submerged in water and to guard against water. Termites are also sensitive to temperature fluctuations. Going deeper underground might help them to maintain an optimal temperature for their colony’s activities, especially after rain has cooled the surface. Going deeper underground may also provide additional protection to the vulnerable stages of the termite life cycle (eggs, larvae, and pupae). In

contrast, ants in arid regions like the Kalahari often seize the opportunity for increased foraging after rain. The moisture enhances the availability of food resources on the surface, such as insects and plant matter. Unlike termites, many ant species build nests with more porous structures (Cosarinsky and Roces, 2007; Tan et al., 2024). Overall, whether the reduction in ants and termites is a general trend across drylands, even after heavy rainfall, or whether it is a localised phenomenon, remains to be investigated through long-term monitoring.

It is not just the impact of climate change on habitats and food sources that threatens the aardvark, but also hunting of aardvarks for traditional medicine and recreation in several countries in Africa (Whittington-Jones et al., 2011). The hunting is driven by an ancient belief among traditional healers that the body parts possess medicinal value (Makwati et al., 2023). Various body parts are also sought after items in traditional medicine and may be used for a variety of purposes including preventing illness, as good luck charms and poison (Kingdon, 1971; Melton, 1976; Makwati et al., 2023). In addition, aardvarks are hunted for bushmeat (Taylor et al., 2016). Illegal hunters use bushmeat both for supplementing household protein and for economic gain (Koutchédi, 2022). For example, the consumption of aardvark meat is considered a delicacy in KwaZulu Natal and has led to an increase in hunting activities that target these animals (Makwati et al., 2023). Hunting wildlife for various purposes carries significant consequences and often results in conflicts between humans and target species (Kingdon et al., 2013; Lindsey et al., 2013). The unsustainable harvesting of aardvarks not only reduces their population numbers but also disrupts the delicate balance of ecosystems in which they play a crucial role.

Similarly, pangolins are subjected to heavy poaching for both local and international markets (IUCN, 2022). In addition to poaching, their habitats have been severely impacted by recent habitat loss (Romero-Muñoz et al., 2020). In certain regions of southern Africa, pangolins are collected from the wild for purposes such as bushmeat and cultural practices, including traditional medicine (Soewu and Sodeinde, 2015). In addition, two more threats that impact pangolins are electrocution on electrified fences and road kill mortalities (Pietersen et al., 2016; Katuwal et al., 2017). A study conducted in South Africa documented 33 individuals electrocuted, including four ground pangolins (Beck, 2009). In

the last five years, there have been 28 reported pangolin deaths and eight instances of electrocuted pangolins on electrified fences. However, it is important to note that many deaths likely go unreported (Pietersen, 2022). Recently, electrified fences in South Africa have been identified as causing the second-highest number of deaths in Temminck's pangolin (Stracquadanio et al., 2024).

Some species are difficult to study because they are either elusive, nocturnal, or found in very low densities. The aardvark and pangolin are animals that are difficult to find and, even on safaris, they are rarely seen. As a result, only a few scientists have attempted to investigate them. It is even more difficult to monitor elusive species especially if doing so over the long-term. There is an urgent need to fill baseline information gaps that will aid in future conservation efforts, such as accurate population estimates, distribution, and the impact of threats. All these gaps require monitoring to detect the animals, which is difficult because they are active at night, their habitat is covered by vegetation making the mammals difficult to spot and experience is required to track their tracks, and they are very sparsely distributed. There are also few methods that have been used with various levels of success on aardvarks and pangolins, such as the use of direct sightings (Dorji, 2017; Ingram et al., 2019), burrow use and spoor (Taylor and Skinner, 2003; Weyer, 2018), holes (Epps et al., 2021), camera traps (Hart et al., 2022) and combining camera trap surveys with IUCN range maps to collect data (Chen et al., 2023). Another method that has not been attempted on either aardvark or pangolin is data collected via social media applications. The method has been shown to be a useful way to potentially collect data on elusive species (Soysal et al., 2016; Di Minin and Hausmann, 2020; Karawita and Perera, 2020; Phakoago et al., 2024).

The use of social media is experiencing a remarkable increase around the world and the widespread use of mobile cameras has increased the observational capacity that can be harnessed for data collection by researchers (Mayer-Schönberger and Cukier, 2013; Ghermandi and Sinclair, 2019; Maritz and Maritz, 2020). Millions of users make use of social media platforms such as Facebook, Instagram, and Twitter by generating billions of posts annually. They generate content that encompasses geotagged text, images, and videos (Kwak et al., 2010; Hausmann et al., 2018). When compared to traditional survey-

based methods, the data from social media can offer a cost-effective means of obtaining information about the activities of rare mammals in protected areas (Di Minin et al., 2015). Social media can also be used for species monitoring, since ecotourists who willingly or involuntarily record sightings of rare or elusive species on the platform serve as citizen scientists (Hausmann et al., 2018). Social media has the potential to address limitations associated with sample size, time, and location constraints, nonresponse bias, and self-reported errors (Mayer-Schönberger and Cukier, 2013).

The present study therefore used social media to collect images of aardvark and pangolin from southern Africa. It was found that social media has the potential to supply supplementary and novel information on the distribution and ecology of elusive species, such as the aardvark and pangolin. The findings also provided insights on the biology of the animals, such as the poor body condition associated with diurnal activity in aardvark (Phakoago et al., 2024; Chapter 4). Very little is known about drinking events of the aardvark or pangolin. However, through the collection of images on social media, the present study showed more water drinking events by the aardvark than in a previous study by Kerley and Tompkins (2017).

Other studies have shown the usefulness of social media to gather information on the distribution and ecology of species. For example, a recent survey of geotagged posts on Twitter and Flickr for the word “pangolin” confirmed the presence of pangolins on earth within the IUCN geographic ranges (Di Minin and Hausmann, 2020), while Instagram posts with the identifiers #monkseal provided information on the Hawaiian monk seal (Sullivan et al., 2019). Social media has also been used to elucidate ecological processes, as shown through a recent study on Facebook records of trophic interactions for southern African herpetofauna as predators and as prey (Maritz and Maritz 2020). Social media also provided new insights about the distribution of snowy owls (*Bubo scandiacus*) in southern and western Europe (Barve, 2014), a bird that is very rarely observed (Hausmann et al., 2018). Two sightings of sperm whales (*Physeter macrocephalus*), a species that is difficult to find from eastern Cyprus in the eastern Mediterranean, were also reported through social media (Snape et al., 2020).

Despite the uncommon sightings of the aardvark and pangolin, indirect measures can also be used, for example burrow density, and droppings, to assess population numbers. Burrow density provides insights into the presence and activity of burrowing species (Castellón et al., 2012; Ingram et al., 2019; Chibowski et al., 2023), while droppings can offer information about health and territorial behaviour, aiding in the identification of species in an area (Putman, 1984; Lioy et al., 2015). Although there are many available methods for monitoring species (Schwarz and Seber, 1999, Williams et al., 2002), few are suitable for scarce mammals or other elusive species (Mills et al., 2000). Many of these methods are either too expensive or not suitable to cover large areas, at least on a regular basis (Link and Sauer, 1997, Zhou and Griffiths, 2007). However, DNA sampling can be used to overcome such challenges for elusive species. For example, the study conducted on common wombats (*Vombatus ursinus*) used microsatellite analysis of faecal DNA to estimate their population size in suburban Melbourne parkland, revealing a population not isolated from others along the Yarra River (Banks et al., 2002). In another study, researchers collected hair samples for DNA analyses of the northern hairy-nosed wombat, *Lasiorhinus krefftii*) to estimate the population size (Banks et al., 2003). These methods are now in widespread use for many elusive burrowing species and could be potentially useful for aardvarks and ground pangolins.

However, the results of Chapter 4 showed that the presence of elusive mammals in arid environments, including the Kalahari, can be detected using burrows. I was able to conduct burrow transects in daytime when the burrowing species were mostly inactive, often when an animal was in the burrow and not actively foraging. Conducting burrow transects in the daytime without disturbance to the animal was possible. In addition, the results in the present study the number of burrows was positively associated with the abundance of grass cover; in an area with low grass cover, the number of burrows was low, and in an area with high grass cover, the number of burrows was high. High grass cover often indicates suitable habitat conditions for various species, as it can offer protection, nesting sites, and foraging opportunities contributing to the overall health and survival of the animals. The presence of burrows within areas of dense grass suggests that the vegetation structure meets the requirements of that burrowing animal. Four other studies have investigated the presence of elusive mammals using burrow transects and environmental

associations (Whittington-Jones et al., 2011; Epps et al., 2021; Mapuru et al., 2021; Makwati et al., 2022). The presence of the aardvark in the Kruger National Park, South Africa, was positively correlated with elevation and vegetation productivity (as measured through a Normalised Difference Vegetation Index [NDVI]) and was negatively correlated with distance to water sources (Epps et al., 2021). Conversely, the presence of aardvarks was influenced by prey abundance at three arid and semi-arid sites in South Africa (Whittington-Jones et al., 2011). The study found that slope did not influence the presence of a burrow, with an equal number of burrows appearing on flat and sloped land (Whittington-Jone et al., 2011). The primary aspect of these burrows was different at each site and varied between north, northeast, and bimodal north/south axis (Whittington- Jones et al., 2011). In contrast, I found more burrows on dunes than flat landscapes and more burrows were west facing than any other orientation. However, Mapuru et al. (2021) found that no environmental variables (including soil type, vegetation, and distance to waterways) influenced burrow placement by the aardvark in Rietvlei Nature Reserve, South Africa. There has been little research on the physical characteristics of pangolin burrows, creating a knowledge gap about the factors that make a burrow suitable for pangolin use.

For burrowing species, burrows serve as a beneficial buffer against climatic conditions, offering heat avoidance during the day and warmth during the night (Milling et al., 2018; Watson et al., 2018). By providing a stable environment, burrows help regulate body temperature and prevent either hyperthermia or hypothermia (Roper et al., 2001; Moore et al., 2018). During winter, I found that the burrow temperature was significantly correlated with time of day, with the burrow warming up in the morning, reaching its highest temperatures between 11h00 am and 17h00 pm. Burrowing mammals return to their warmer burrows in the evening during winter, using burrows as a buffer against the effect of the cold air temperatures at night (Weyer et al., 2020). In addition, burrowing mammals remain in their cooler burrows during summer to avoid high air temperatures during the day (Pike and Mitchell, 2013; Milling et al., 2018).

To understand the impact on aardvarks and pangolins or other myrmecophagous mammals, or other mammals that feed on insects, there is a need to establish a continuous

monitoring system to track their populations in the Kalahari region. By closely monitoring the shifting distribution of these species over time, any changes in their presence and abundance can be identified. In addition, it is essential to assess if these mammals adapt to new areas, modify their behaviour, and adapt to land-use changes because of agriculture. Sustainable agricultural practices should balance food production with conservation. The impacts of extensive burning practices in reserves should also be investigated. Mitigation strategies should be developed to address challenges and sustain farming practices.

Understanding an ecosystem's response to climate change requires collaboration among multiple teams and organisations with diverse expertise and resources. By working together, collaborators can combine knowledge and resources to better understand how climate change will affect the ecosystem and its inhabitants. Collaboration enhances efficiency through shared resources and experience. For example, researchers with diverse expertise can monitor species across trophic levels to combat the impact of climate change in a form of a long-term monitoring of species. Research institutions can provide valuable scientific data and analysis, while conservation organisations can implement on-the-ground conservation actions and engage local communities (Fancy and Bennet, 2012). Studying interactions between species helps scientists to understand how climate change affects ecosystem balance, informing conservation and management strategies. Furthermore, by monitoring changes in trophic levels over time, researchers can identify early warning signs of ecosystem collapse and take proactive measures to prevent irreversible damage. In addition, this interdisciplinary approach to studying climate change can also lead to the development of innovative solutions, such as sustainable agriculture practices and alternative energy sources, that can help us adapt to a changing world.

As with any research project, the sustainability of each project depends on funding. Without adequate financial support, it becomes challenging to conduct in-depth studies, analyse data, and draw meaningful conclusions. Government grants, private donations, and corporate sponsorships are all vital sources of funding for research projects. Securing funding requires a proposal that outlines the goals of the project, the methodology that will be used, and the potential impact of the research. It is essential for researchers to

demonstrate the significance of their work and how it aligns with the funding organisation's priorities and interests. In addition to securing initial funding, researchers must also consider long-term sustainability. Seeking additional funding sources, forming partnerships with other organisations, or exploring alternative revenue streams is important in research. Sustainability is crucial for ensuring that research projects can continue to make a meaningful contribution to their respective fields and address important societal issues.

The value of long-term ecological monitoring is widely acknowledged, yet maintaining such datasets can pose significant challenges. For example, fluctuations in funding can make it difficult to secure the resources necessary to continue to collect and analyse data over time (Silvertown et al., 2006; Magurran et al., 2010; Lindenmayer et al., 2012). Without consistent financial support, monitoring programs may be forced to scale-back operations, reduce sampling frequency, or even shut down entirely, putting data at risk. Recent events such as the COVID-19 outbreak have exacerbated funding difficulties. However, climate change, being a significant global threat, emphasizes the need for funding support to acquire essential research equipment for continuous, quality data collection. While some equipment such as weather stations can be purchased once and then used indefinitely, with servicing, others require regular replacement. The purchase of animal tracking devices is not a once-off exercise, partly because they require regular replacement due to limited battery life and memory capacity, and because they can be lost or damaged through animal activities, and the technology keeps improving making newer devices more attractive. Sustained funding is required to ensure the availability of resources for ongoing monitoring efforts.

Sharing long-term data among researchers and experts in the field is also essential when studying the impacts of climate change on animal populations. Sharing data will enable researchers to track long-term trends and observations across various regions and ecosystems. Conducting research in various regions within species distribution ranges enhances knowledge and provides insights into whether similar species respond similarly to climate change over time. Cooperative long-term research projects contribute to the development of conservation strategies based on geographic niche findings. Long-term studies also offer trends on ecosystem recovery from extreme occurrences, helping

evaluate the effects on ecosystems and refine conservation methods (Howard and Dixon, 1990; Karley et al., 2004). Various methodological approaches applied through collaborative work contribute to a comprehensive understanding of ecosystem dynamics and effective conservation strategies (Staudt et al., 2013).

For example, much of the research around the world in the last decade has focused on mitigation measures for combating the illegal trade of pangolins, a trade which is largely unsustainable (Pires et al., 2016; Wallen and Daut 2018; Challender and O'Criodain, 2020; Huang et al., 2021; Sharma et al., 2020; Tinsman et al., 2023). For the aardvark, there have been some reports on habitat loss from agricultural development and the illegal wildlife trade (Lindsey et al., 2013; Koutchédi, 2022). Although poaching and hunting have been mentioned as threats to the aardvark and pangolin (Heighton and Gaubert, 2021; Makwati et al., 2023), climate change serves as an emerging potential threat to both mammals. A combination of conservation strategies that address habitat protection, combat illegal trade, and promote climate change awareness are key measures to help protect these species. There is a need to establish and protect either conservation areas or reserves that encompass the suitable habitats of the aardvark and pangolin for their survival. Land-use planning should consider their ecological needs to prevent habitat loss (Powers and Jetz, 2019). Strengthening law enforcement, increasing penalties for wildlife trafficking, and involving local communities in conservation efforts are essential. Campaigns can help identify threats and promote coexistence with these species (Nyhus, 2016).

The potential extinction of the aardvark and pangolin poses a serious threat to the various ecosystems that they inhabit. The aardvark and pangolin play several important roles in their ecosystems by controlling insect populations, shaping plant communities, contributing to nutrient cycling, serving as food sources for other predators and creating burrows. Overabundance of insects without the presence of myrmecophagous can cause a ripple effect throughout the food chain, causing habitat degradation due to overharvesting of grasses by ants and termites (Branson et al. 2006; Jaworski and Hilszczanski 2013), leading to imbalances and disruptions that could have far-reaching consequences (Kairis et al., 2015). For example, the aardvark and pangolin are known to consume vast

quantities of insects, which helps to control the populations of those insects. Previous studies in the Kalahari recorded on average ~15,400 ants and termites eaten by a pangolin per night which can be extrapolated to ~5.6 million ants and termites per year (Panaino, 2021). The aardvark, on average, consumed ~37,000 termites per night, which can be extrapolated to ~13.5 million termites per year (Weyer, 2018). In the absence of myrmecophagous species, an overabundance of insects could cause habitat deterioration by the overharvesting of vegetation (Jaworski and Hilszczanski 2013), which can lead to ecological imbalance (Whittington-Jones et al., 2011; Kairis et al. 2015; Martin, 2017; Challender et al., 2019; Pietersen et al., 2020). Myrmecophagous mammals contribute to nutrient cycling by distributing nutrients through their faeces that enrich soil quality and influence plant growth (Beca et al., 2022). Further studies need to be conducted to quantify the importance of the aardvark and pangolin in an ecosystem, with a focus on the foraging behaviour to quantify the ecosystem services that they provide when it comes to soil turnover, and biodiversity accumulation in foraging sites. In addition, the potential loss of the aardvark could disproportionately affect species that are dependent on aardvark activity for refuge and reproduction via the provision of burrows (Dean and Siegfried, 1991; Taylor and Skinner, 2000; Skinner and Chimimba, 2005). The aardvark and pangolin also have cultural significance to indigenous communities (Fopa et al., 2020; Mouafo et al., 2021). The loss of the aardvark and pangolin would represent a loss of cultural heritage and knowledge (Baiyewu et al., 2018).

The conservation status of many species in the wild is unknown due to a lack of quantitative data on their population numbers. The aardvark and Temminck's pangolin are no exception. Without accurate information on the current population sizes and population trends of these animals in the wild, it becomes difficult for conservationists and researchers to develop effective strategies for their protection. The IUCN considers the aardvark to face no immediate threat, in contrast to what the recent work on the responses of aardvark to droughts shows (Rey et al., 2017; Weyer et al., 2020). As such, there is a need to conduct comprehensive investigations into the population numbers of the aardvark and Temminck's pangolin in order to fill this critical knowledge gap and to establish ways to conserve the habitat of the aardvark and Temminck's pangolin. Understanding animal densities helps in monitoring population trends over time, identifying potential threats, and

implementing effective conservation measures. By so doing, a more sustainable future for the aardvark and Temminck's pangolin can be established, ensuring that these unique and valuable species are preserved for future generations.

There is also still much to be learnt about how various life stages impact the survival of mammals facing climate change. For example, young Temminck's pangolins are known to disperse, but no studies have been undertaken to assess how they disperse, where they go, how far they go, and what proportion survive until adulthood. Previous observations (MV Phakoago, unpublished data) indicated that young Temminck's pangolins disperse over substantial distances, a feat that will require substantial energy intake to support the cost of moving away from their mother's home range. They may also encounter electrified fences around reserves. Young pangolins likely would fall prey to a variety of predators as their scales are still comparatively soft and their smaller size makes them easier to be processed by a predator than adult pangolins with hard scales. The present study intended to investigate the impacts of changes in the environment on juvenile pangolins. Unfortunately, a severe drought before the investigation started led to pangolins starving and producing no young (Panaino W, unpublished data). Little is known about young aardvarks too; there are very few observations of juvenile aardvarks and there are also none in the social media records. Understanding the ecology and dispersal of juvenile pangolins and aardvarks, and how they survive under changing environmental conditions, is vital for effective conservation of these species. Biologists need to shift their focus from adult animals to include juveniles, and the research methods developed in the present study could help in the endeavour.

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Appendix

List of figures

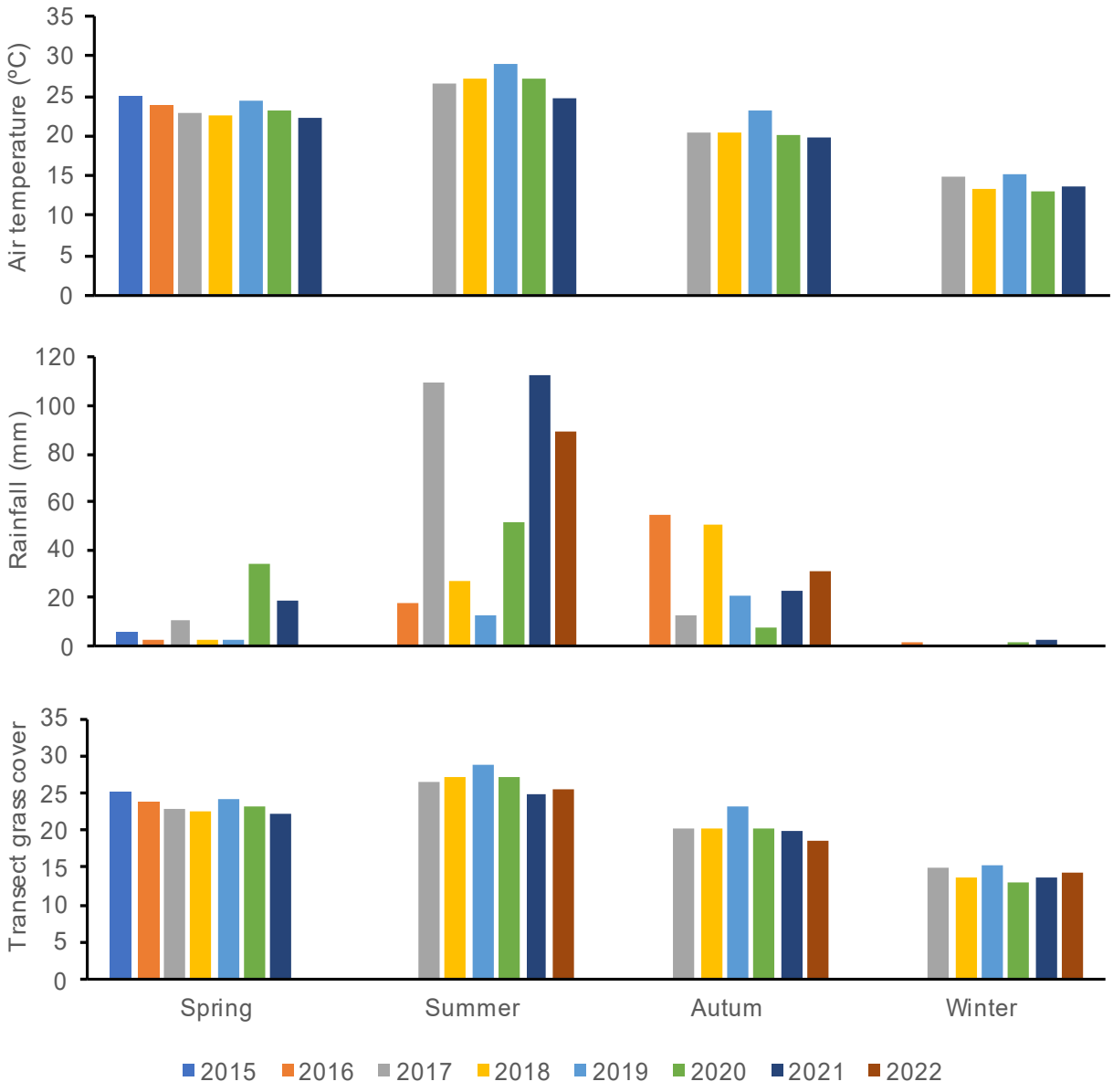

Figure A1: Mean seasonal records of mean air temperature, rainfall, and grass cover at Tswalu Kalahari Reserve, Northern Cape Province, South Africa between 2015 and November 2022.

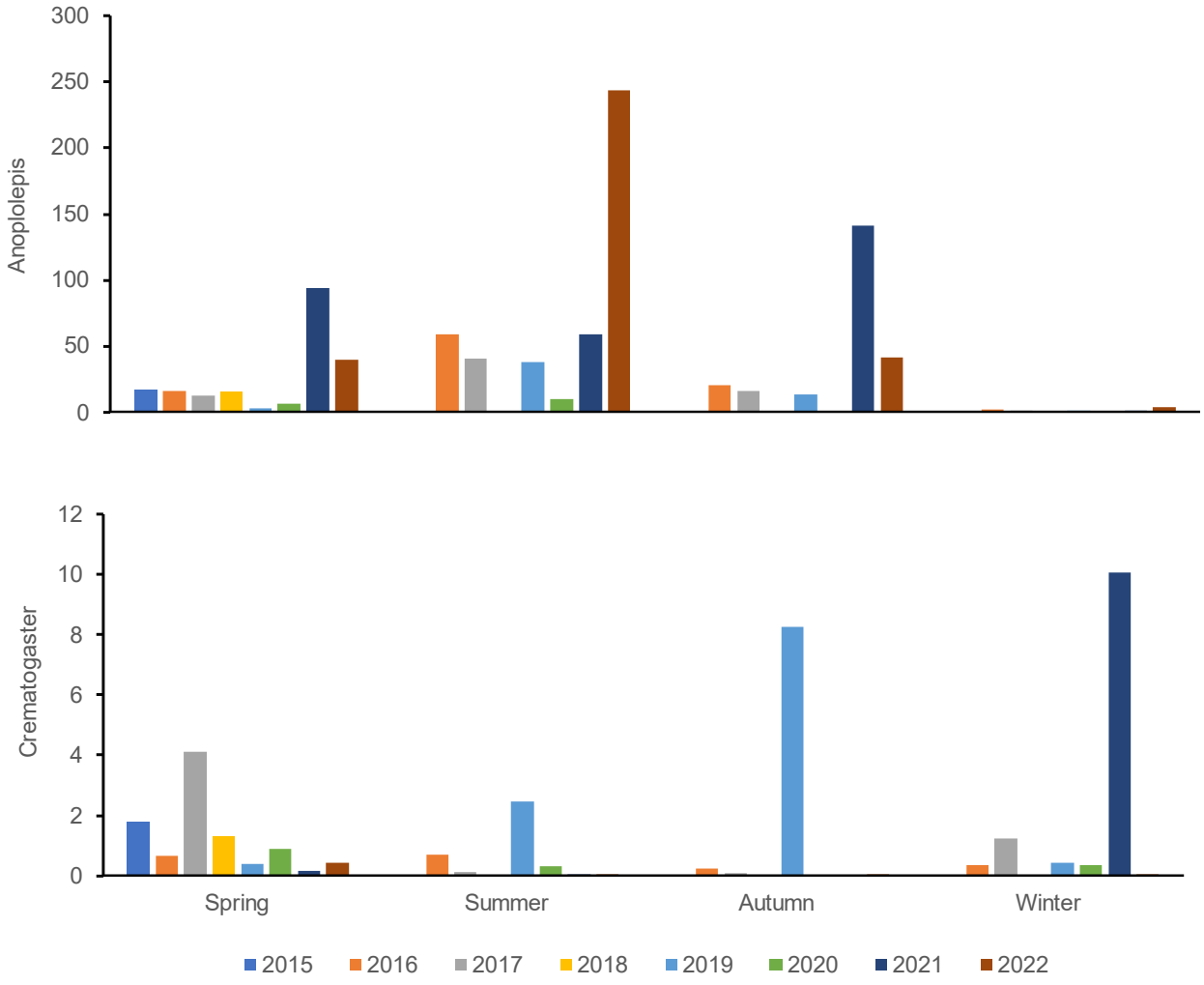

Figure A2: Mean seasonal records of ants (*Anoplolepis* and *Crematogaster*) per trap at Tswalu Kalahari Reserve, Northern Cape Province, South Africa between September 2015 and August 2022.

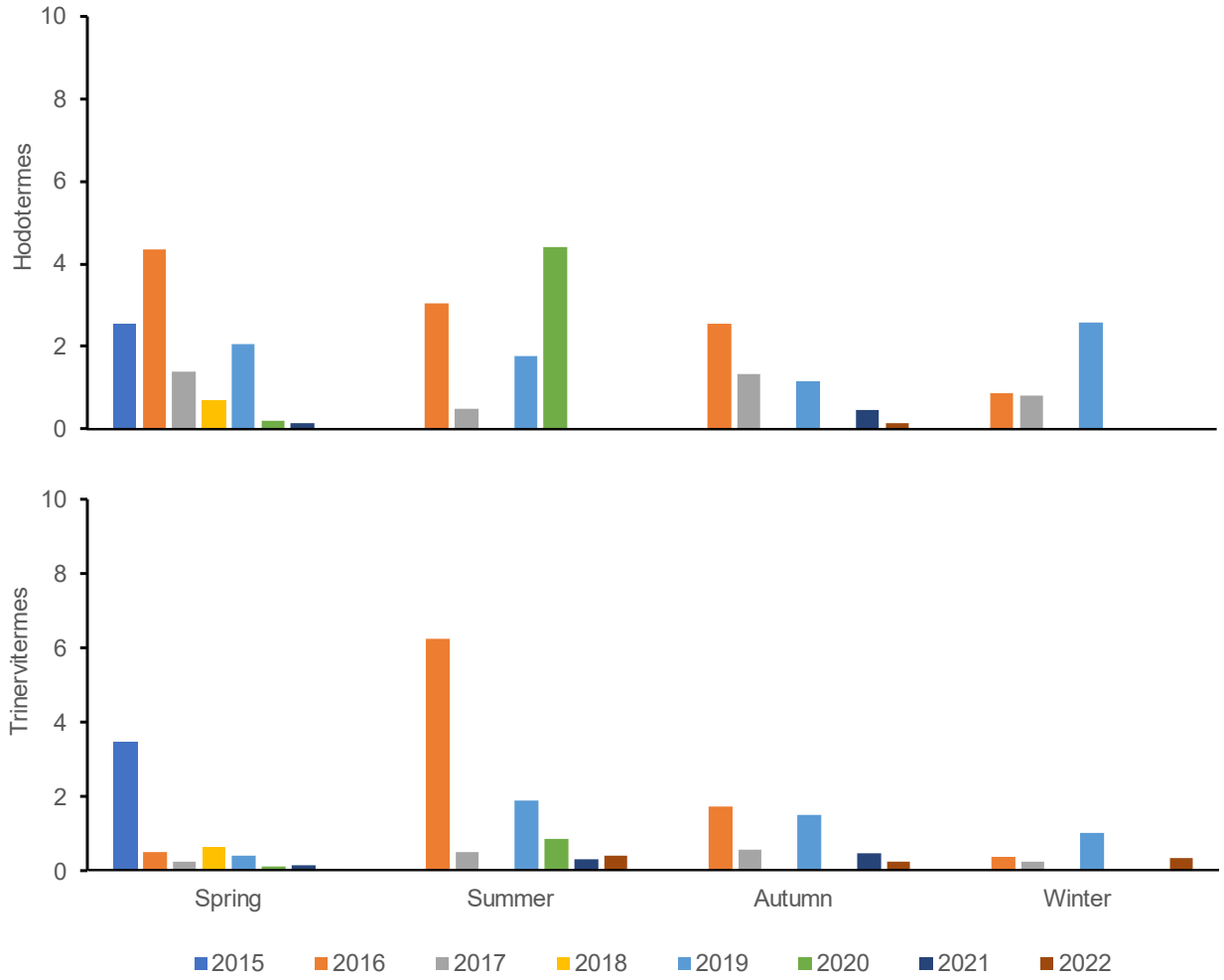

Figure A3: Mean seasonal records of termites (*Hodotermes* and *Trinervitermes*) per trap at Tswalu Kalahari Reserve, Northern Cape Province, South Africa between September 2015 and August 2022.

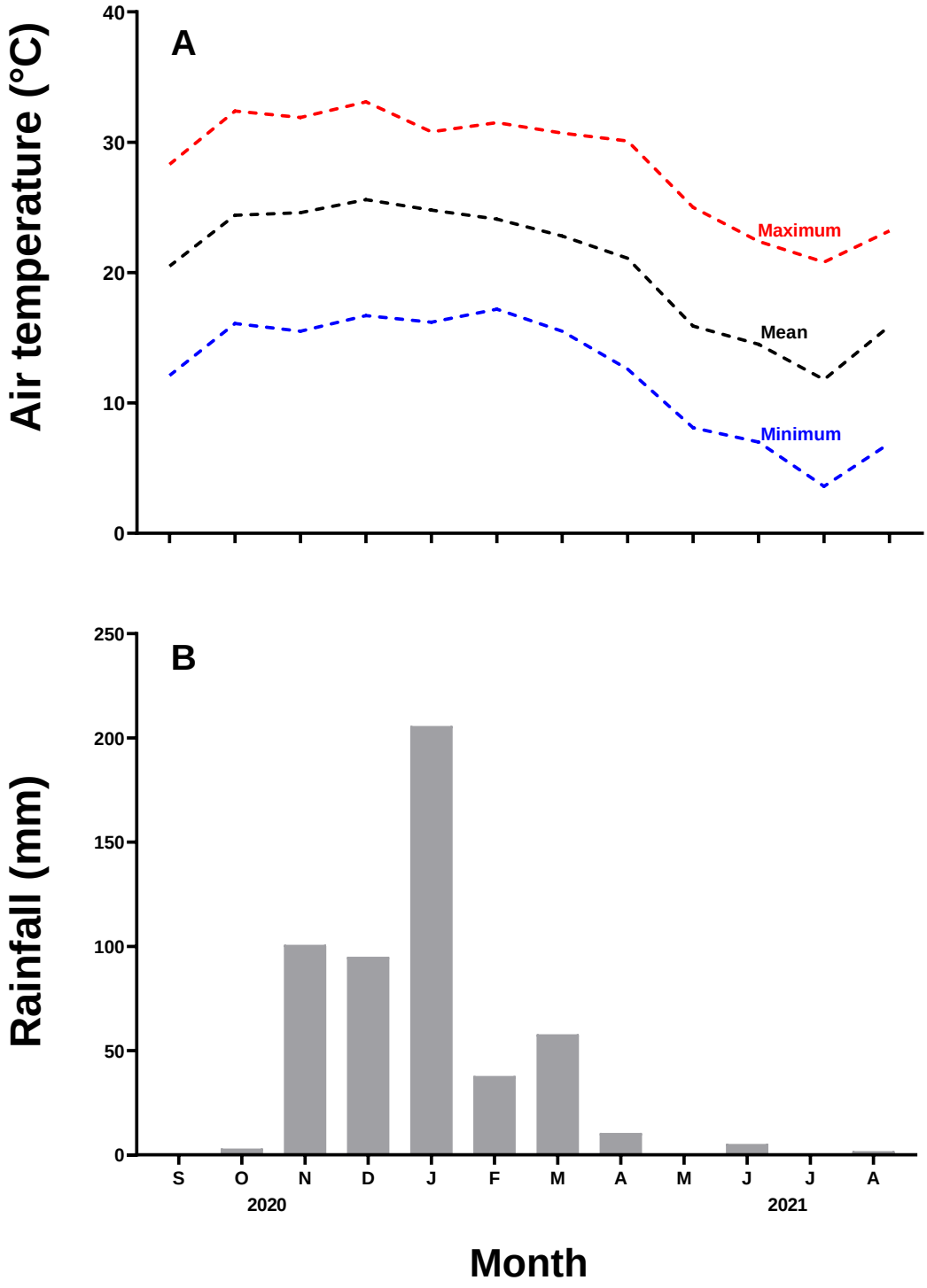

Figure A4 A) Mean monthly air temperature and, B) rainfall (mm) across 33 rain gauges on Tswalu Kalahari Reserve, Northern Cape Province, South Africa, between September 2020 to August 2021.

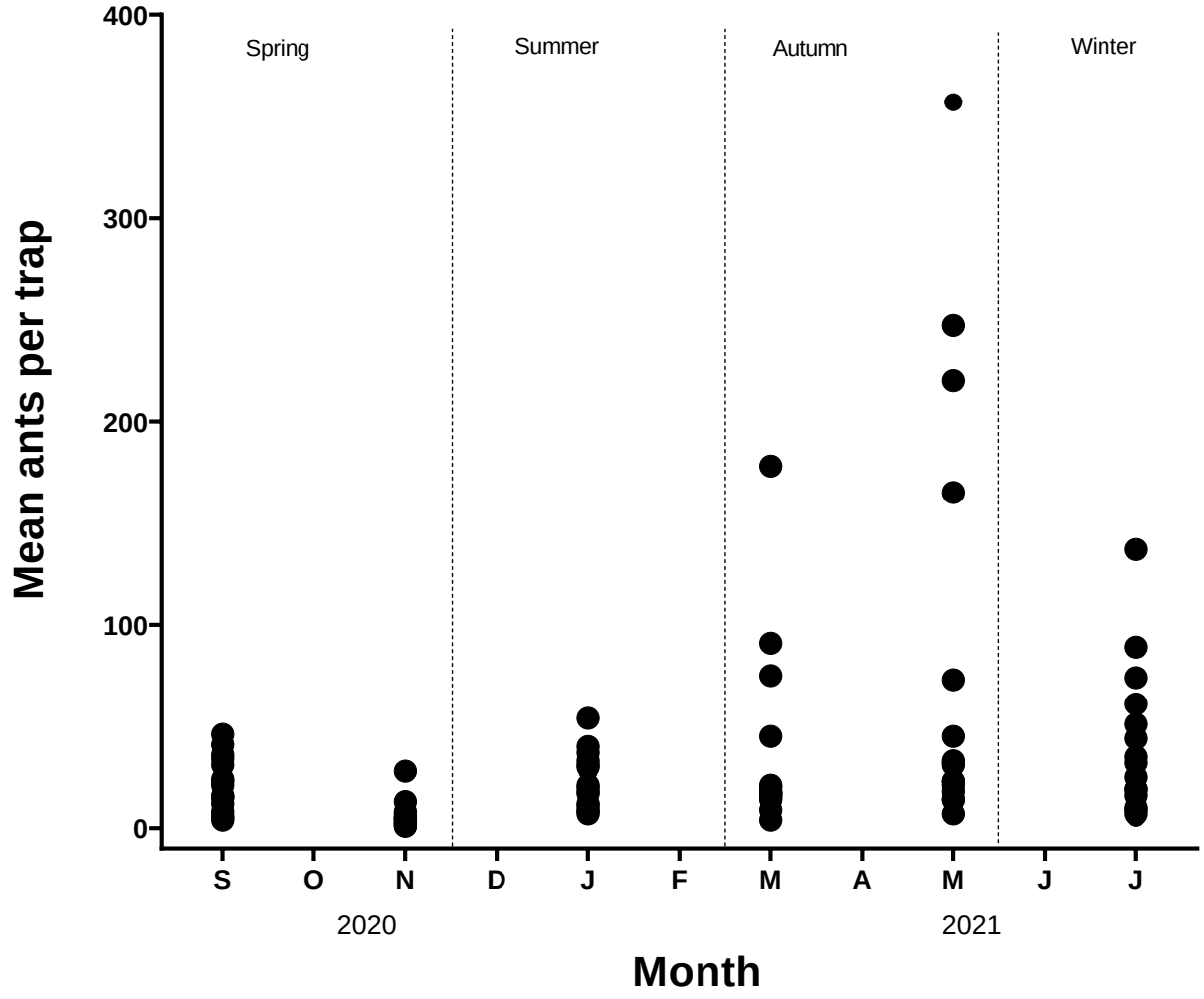

Figure A5. The seasonal variation in the mean number of ants per trap across the study period between September 2020 to July 2021 at Tswalu Kalahari Reserve, Northern Cape Province, South Africa. Ant trapping data were collected monthly, and grouped into seasons (summer, autumn, winter, spring). The graph presents the average number of ants abundance captured per trap for each month, providing insights into seasonal trends in ant activity within the study area.

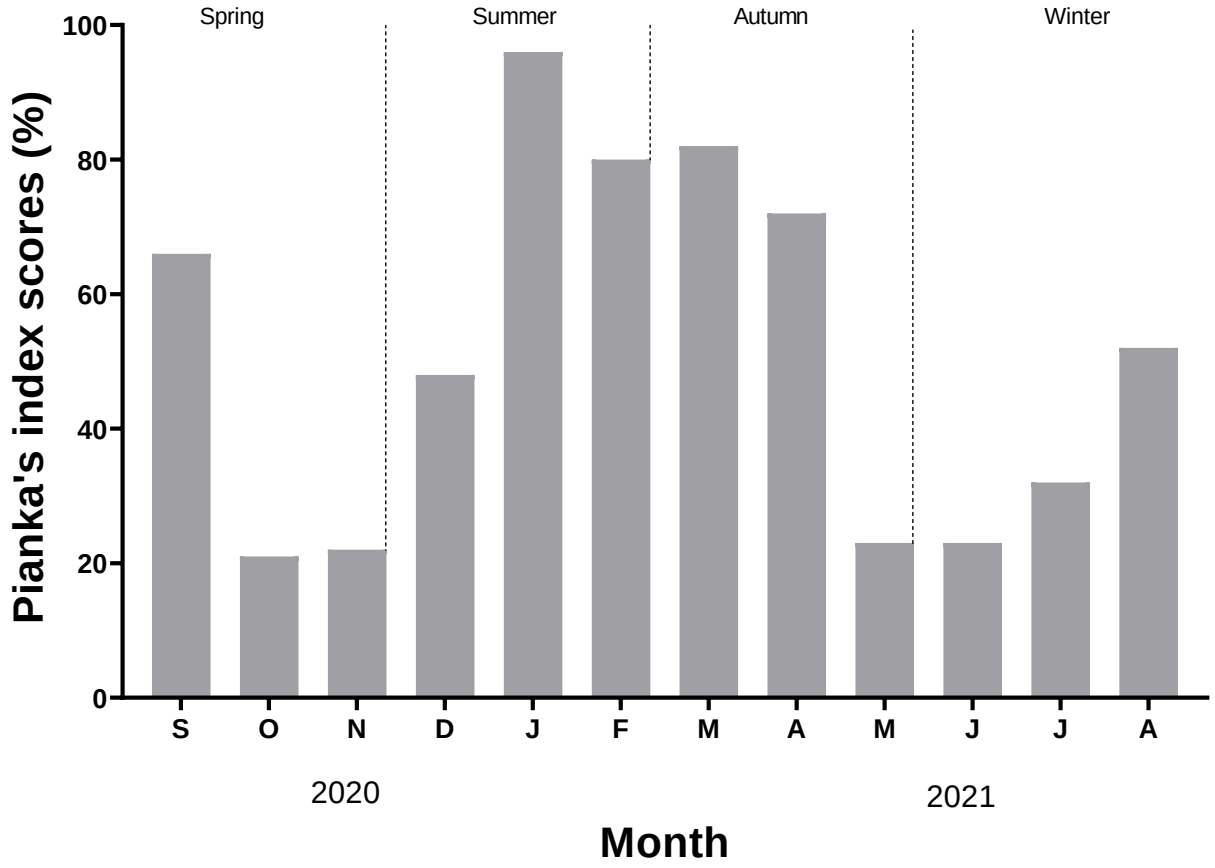

Figure A6. The seasonal dietary overlap between aardvark (*Orycteropus afer*) and pangolin (*Smutsia temminckii*), measured using Pianka's index, for each month throughout the study period at Tswalu Kalahari Reserve, Northern Cape Province, South Africa. Pianka's index values range from 0 to 1, where 0 indicates no overlap and 1 indicates complete overlap in dietary resources. The data for each month is grouped into seasons (spring, summer, autumn, and winter) to show how the overlap varies across different times of the year. Each point represents the Pianka's index value for a specific month, with seasonal trends highlighted to provide insights into how the abundant and consumption of dietary resources by these two species change with the seasons.

Aardvark	Pangolin
Aardvark, erdvark, earthpig, anteater, Orycteropus, afer, aardvarksafaris, aardvark sightings, aardvark photos	Pangolin, ground pangolin, scaly anteater, ietermagog, Smutsia, temminckii, pangolinphotosafaris, pangolin safaris, pangolin photos, pangolin sightings

Figure A7: Search terms for aardvark (*Orycteropus afer*) and pangolin (*Smutsia temminckii)* images and videos on Facebook and Instagram.

Table A1: Model selection of best fit based on Akaike Information Criterion (AIC) values for the effects of accumulated rainfall three, two, and one month prior to conducting transects surveys, as well as during the same month in which transects were surveyed and which variable to use in the linear mixed model that influences grass cover at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

	AIC	**ΔAIC**
Rainfall 3 months prior	407.36	0.00
Rainfall 1 month prior	417.57	10.21
Rainfall 2 months prior	430.43	23.06
Rainfall same month	435.09	27.72

Table A2: The linear mixed model of the effect of rainfall that fell three months prior on grass cover at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

Parameter	**Coefficient**	**Standard error**	**95% CI**	***t***	***P***
Intercept	17.83	0.71	[16.48, 19.27]	72.33	<0.001
3 months	1.00	7.30e-04	[1.00, 1.00]	3.86	<0.001

Table A3: Model selection of best fit based on Akaike Information Criterion (AIC) values for the effects of air temperature and grass cover on *Anoplolepis* ants at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

	AIC	**ΔAIC**
Minimum air temperature	1875.46	0.00
Mean air temperature	2076.58	201.11
Maximum air temperature	2110.20	234.73

Table A4: Model selection of best fit based on Akaike Information Criterion (AIC) values using linear mixed model for the effect of minimum air temperature and grass cover on *Anoplolepis* ants at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

Parameter	**Coefficient**	**Standard error**	**95% CI**	***t***	***P***
(Intercept)	0.62	0.09	[0.47, 0.82]	-3.35	<0.001
Minimum air temperature	1.18	8.80e-03	[1.16, 1.19]	21.73	<0.001
Grass cover	1.06	2.27e-03	[1.06, 1.06]	27.20	<0.001

Table A5: Model selection of best fit based on Akaike information criterion values to determine air temperature variable on *Crematogaster* ants at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

	AIC	**ΔAIC**
Maximum air temperature	161.71	0.00
Mean air temperature	165.80	4.09
Minimum air temperature	171.14	9.43

Table A6: Model selection of best fit based on Akaike Information Criterion (AIC) values using linear mixed model for the effect of maximum air temperature, grass cover and rainfall on *Crematogaster* ants at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

Parameter	Coefficient	Standard error	95% CI	*t*	*P*
(Intercept)	72.02	81.27	[7.62, 641.21]	3.79	<0.001
Maximum air temperature	0.90	0.03	[0.83, 0.97]	-2.87	0.004
Rainfall	0.98	0.01	[0.94, 1.00]	-1.42	0.155
Grass cover	0.95	0.02	[0.91, 0.99]	-2.37	0.018

Table A7: Model selection of best fit based on Akaike Information Criterion (AIC) values to determine temperature variable on *Hodotermes* termites at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

	AIC	ΔAIC
Maximum air temperature	117.70	0.00
Mean air temperature	119.40	1.70
Minimum air temperature	120.99	3.29

Table A8: Model selection of best fit based on Akaike Information Criterion (AIC) values using linear mixed model of the effect of maximum air temperature and grass cover on *Hodotermes* termites at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

Parameter	Coefficient	Standard error	95% CI	*t*	*P*
(Intercept)	1.62	2.19	[0.10, 19.97]	0.35	0.723
Maximum air temperature	1.03	0.04	[0.96, 1.11]	0.73	0.468
Grass cover	0.92	0.03	[0.87, 0.97]	-2.88	0.004

Table A9: Model selection of best fit based on Akaike Information Criterion (AIC) values to determine temperature variable on *Trinervitermes* termites at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

	AIC	**ΔAIC**
Maximum air temperature	32.86	0.00
Mean air temperature	33.17	0.31
Minimum air temperature	33.71	0.85

Table A10: Model selection of best fit based on Akaike Information Criterion (AIC) values using linear mixed model of the effect of maximum air temperature and grass cover on *Trinervitermes* termites at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

Parameter	**Coefficient**	**Standard error**	**95% CI**	***t***	***P***
(Intercept)	0.11	0.47	[0.00, 87.02]	-0.52	0.604
Maximum air temperature	1.09	0.12	[0.91, 1.41]	0.79	0.429
Grass cover	0.85	0.10	[0.63, 1.00]	-1.36	0.175

Table A11: Model selection of best fit based on Akaike Information Criterion (AIC) results to determine the effects of accumulated rainfall three, two, and one month prior to conducting transects, as well as during the same month in which transects were conducted. The model with rainfall accumulated over three months prior had the lowest AIC value, indicating the best fit (AIC = 0.88, ΔAIC = 0.00) at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

	AIC	**ΔAIC**
3 months	0.88	0.00
1 month	0.00	10.37
Same month	0.03	6.77
2 months	0.09	4.64

Table A12: Results of the generalised linear mixed model of the effect of total rainfall that fell three months prior to the sampling date on grass cover at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

Parameter	**Coefficient**	**Standard error**	**95% CI**	***t***	***P***
Intercept	$2.07x10^{9}$	$6.50x10^{9}$	$4.44x10^{6}$, $9.69x10^{11}$	6.84	<.001
3 months	1.28	0.10	(1.10, 1.48)	3.28	0.001

Table A13: Results of the generalized linear mixed-effects model that assessed seasonal variation in grass cover. Significant seasonal variations in grass cover were observed, with higher cover in autumn, winter, and spring compared to summer ($P < 0.001$) at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

Parameter	**Coefficient**	**Standard error**	**95% CI**	***t***	***P***
Intercept	1.54	0.30	[1.04, 2,26]	2.19	0.030
Summer	-	-	-	-	-
Autumn	11.28	2.70	[7.02, 18.12]	10.12	<0.001
Winter	10.42	2.88	[6.03, 18.03]	8.48	<0.001
Spring	3.35	0.80	[2.09, 5.37]	5.09	<0.001

Table A14: Pairwise contrasts of estimated log-scaled, Turkey-adjusted marginal means for grass cover. Significant differences in grass cover were found for most seasonal comparisons ($P < 0.0001$), except for autumn versus winter ($P = 0.9878$) at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

Contrast	**Estimate**	**Standard error**	**df**	***t***	***P***
Summer-autumn	-2.4226	0.239	112	-10.117	<.0001
Summer-winter	-2.3442	0.277	112	-8.478	<.0001
Summer-spring	-1.2097	0.237	112	-5.094	<.0001
Autumn-winter	0.0784	0.239	112	-0.327	0.9878
Autumn-spring	1.2129	0.193	112	6.282	<.0001
Winter-spring	1.1345	0.237	112	4.778	<.0001

Table A15: Results of the generalized linear mixed-effects model with a negative binomial link function for seasonal differences in prey abundance. The model accounts for random effects due to repeated measures within sampling sites and individual variability at Tswalu Kalahari Reserve, Northern Cape Province, South Africa. CI=Confidence Interval.

Characteristics	**Incidence rate ratio**	**95 % CI**
(Intercept)	20.16	15.43, 26.33
Season		
Summer	-	-
Autumn	2.28	2.06, 2.53
Winter	1.47	1.31, 1.66
Spring	0.58	0.51, 0,66

Table A16: Pairwise contrasts of estimated log-scaled, Turkey-adjusted marginal means for prey abundance. The table shows the contrasts between different seasons, including the ratio, standard error, and p-value for each comparison. All contrasts show significant differences ($P < 0.0001$) at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

Contrast	**Ratio**	**Standard error**	***P***
Summer-Autumn	-15.831	0.0521	<0.0001
Summer-winter	-6.358	0.0610	<0.0001
Summer-spring	8.575	0.0637	<0.0001
Autumn-winter	9.848	0.0443	<0.0001
Autumn-spring	28.545	0.0480	<0.0001
Winter-spring	16.284	0.0574	<0.0001

Table A17: Model selection of best fit based on Akaike Information Criterion (AIC) results to determine the effects of accumulated rainfall three, two, and one month prior to conducting transects on the dietary overlap for aardvarks *Orycteropus afer*) and pangolins (*Smutsia temminckii*), as well as during the same month in which transects were conducted at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

	AIC	**ΔAIC**
2 month	114.80	0.00
1 month	115.72	0.92
Same month	118.49	3.70
3 month	119.48	4.68

Table A18: Results of the generalised linear mixed model of the effect of rainfall that fell two months prior to the sampling date on the dietary overlap between aardvarks *Orycteropus afer*) and pangolins (*Smutsia temminckii*) at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

Parameter	**Coefficient**	**Standard error**	**95% CI**	***t***	***P***
Intercept	3.49e+16	3.06e+17	<0.0001	4.35	<.001
Rainfall	1.34	0.14	(1.08, 1.65)	2.69	0.007

Table A19: Multiple linear regression results of the effects of total rainfall two months prior on grass cover and prey abundance. Significant effects were observed for the intercept ($P < 0.001$) and rainfall two months prior ($P = 0.012$) at Tswalu Kalahari Reserve, Northern Cape Province, South Africa.

Parameter	**Coefficient**	**Standard error**	**95% CI**	***t***	***P***
Intercept	$3.75x10^{30}$	$7.29x10^{31}$	[$1.08x10^{14}$, $1,30x10^{47}$]	3.62	<0.001
Grass	0.06	0.10	[0.00, 1.80]	-1.62	0.105
Prey abundance	1.01	0.61	[0.31, 3.33]	0.02.	0.981
2 months rainfall	1.36	0.17	[1.07, 1.74]	2.52	0.012

ANIMALS RESEARCH ETHICS COMMITTEE (AREC)

UNIVERSITY OF THE WITWATERSRAND, JOHANNESBURG

STRICTLY CONFIDENTIAL

CLEARANCE CERTIFICATE NUMBER: 2020/09/06/C

APPLICANT: Ms MV Phakoago

School: School of Physiology; Department: N/A; Location: Tswalu Kalahari Reserve, Northern Cape

PROJECT TITLE: Myrmecophagous mammals in a changing world: population densities, habitat preference, and activity patterns of aardvarks (*Orycteropus afer*) and ground pangolins (*Smutsia temminckii*) in the Kalahari.

Category: C; Species and Numbers involved: *8X female, 6X male and 6 - 8 juveniles, all 1kg , Ground Pangolins (Smutsia temminckii) and unspecified number of male/female Ground Pangolin + Aardvark (Smutsia temminckii and Orycteropus afer)*

Approval is hereby given for the use of animals for the research project named above and described in the application reviewed by a quorate meeting of the AREC held on 29 Sep 2020. This approval remains valid until 2 Dec 2022 and is conditional to the following (if blank there are no special conditions):

Condition 1	Condition 2	Condition 3	Condition 4
ensure all permits are in place before the commencement of the study			

All material changes to the approved research must be reported to the AREC before they are implemented. Failure to do so will invalidate this clearance certificate.

An annual progress report must be provided to the AREC.

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

I, the Chair of the AREC (or my designated representative) am satisfied that the proposed research is ethical as judged by local law, international standards and University policy.

Signed: _____ _____ Date: _____04/12/2020____

(Chairperson of the AREC)

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

CC: Student supervisor: «Title1» «Initials1» «Supervisor_surname»
Director Central Animals Service: Dr Kim Jardine

Signed: __ _____ Date: __04/12/2020_____

(Registered Veterinarian)

CC: Student supervisor: «Title1» «Initials1» «Supervisor_surname»
Director Central Animals Service: Dr Kim Jardine