The ecological role of Temminck's pangolins in a dryland ecosystem

by

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DECLARATION

I, Daniel L. Rossouw, declare that “**The ecological role of Temminck’s pangolins in a dryland ecosystem**” is my own work, that has not been submitted for any degree or examination at any other university, and that all the sources I have used or quoted have been indicated and acknowledged by means of complete reference.

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ABSTRACT

Conservation practices prioritising the preservation of species, along with the ecosystem services that they provide, are crucial as threats to global biodiversity escalate. Rare species are often assumed to have a limited contribution to overall ecosystem functionality, yet these species are often the most in need of conservation efforts. However, the extent to which rare species contribute to ecosystem processes remains poorly understood. One such species is Temminck's pangolin (*Smutsia temminckii*), which has been speculated to impact ecosystem functionality through contributions to soil turnover, increases in local biodiversity and nutrient cycling. The International Union for the Conservation of Nature (IUCN) has classified Temminck's pangolins as Vulnerable due to their decreasing population trend, largely as a result of their exploitation in the illegal wildlife trade. Temminck's pangolins are recognised globally as a threatened mammal requiring urgent protection. Despite their threatened status, the consequences of their loss in terms of ecosystem services are poorly understood, and empirical data on their ecological role is limited. Therefore, the aim of my study was to gain an understanding of Temminck's pangolin foraging behaviour and patterns (foraging frequency and distance foraged) and evaluate the ecosystem services these pangolins provide through their foraging activities. I opportunistically located four Temminck's pangolins at Tswalu Kalahari Reserve, Northern Cape, South Africa, and tagged each with a Very High Frequency (VHF) tracking transmitter. I observed pangolins during their foraging activities, and recorded data for the seasonal frequency of foraging sites created, the distance travelled while foraging, and how foraging frequency and distance foraged may be affected by prey abundance. I took measurements of seasonal soil turnover, accumulated organic matter and soil nutrient concentration at foraging digs, with repeat samples being taken for biodiversity accumulation and nutrient concentration to assess changes over time. The mean foraging frequency of pangolins was 12.5 ± 7.3 sites per hour and varied seasonally, with peaks in summer (17.9 ± 4.4 sites per hour) and winter (14.4 ± 9.7 sites per hour) as compared to lower values in autumn (11.3 ± 6.3 sites per hour) and spring (8.5 ± 3.9 sites per hour). The mean distance foraged per hour, 0.2 ± 0.1 km, did not differ seasonally. Prey abundance showed seasonal variation, increasing in summer (28.7 ± 23.2 ants per trap) and autumn (27.0 ± 28.1 ants per trap) and decreasing in winter (13.7 ± 17.3 ants per trap) and spring (13.4 ± 13.1 ants per trap). Prey abundance was 115 % higher in summer as compared to in spring. Foraging frequency was not linked to prey abundance, however, the distance foraged was positively associated with prey abundance. The results of my study provide support for seasonal variability in pangolin foraging behaviour, and its potential link to prey abundance. I estimated that a single pangolin uses 29 855 ± 8281 foraging sites each year, turning over 15.6 ± 10.8 metric tonnes of soil (15 619 ± 10 788 kg), and that their foraging digs accumulate 66.1 ± 62.8 kg of organic matter each year. Pangolin foraging had no effect on the nitrogen concentration of soil throughout the year, with mean concentrations of 0.03 ± 0.01 % in both dig sites and control sites. In contrast, the total carbon concentration was 10.4 % (relative difference) higher in the soil of pangolin dig sites (0.20 ± 0.07 %) as compared to the surrounding undisturbed soils (0.19 ± 0.05 %). The ecosystem services of Temminck's pangolins, quantified in my study, are comparable to those of Chinese pangolins (*Manis pentadactyla*), however Temminck's pangolins may provide additional services, such as burrow maintenance and altering plant community structure. Soil turnover estimate for Temminck's pangolins, when expressed relative to body mass (2.6 tonnes of soil individual^{-1} kg body mass^{-1} year^{-1}), align with estimates for fossorial animals in general (1.8 to 3.6 tonnes of soil individual^{-1} kg body mass^{-1} year^{-1}). Overall, my study demonstrates that pangolins contribute to their environment through the ecosystem services that they provide. By quantifying the ecosystem services of Temminck's pangolins, my study may allow for better alignment of conservation efforts to protect this vulnerable species and preserve their unique and vital role within the ecosystem.

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CHAPTER 1

General introduction

Biodiversity is threatened on a global scale by natural and anthropogenic influences such as habitat loss, fragmentation, transformation, and overexploitation from the illegal wildlife trade (Prakash and Verma, 2022). Ecosystem stability is directly affected by loss of biodiversity, as the capturing of essential resources, production of biomass, decomposition, and recycling of essential nutrients by ecological systems is compromised, diminishing the overall stability of the ecosystem (Cardinale et al., 2012). An emerging trend in conservation practices is to prioritise the preservation of species along with the ecosystem services that they provide, especially in ecosystems that are at high risk of being compromised (Egoh et al., 2007). One such range of ecosystems are those with low rainfall climates, such as the Kalahari region of southern Africa, where my study was conducted. It is predicted that these regions will continue to experience rising air temperatures, increased evapotranspiration, and alterations in rainfall patterns, impacting resource availability (Engelbrecht et al., 2015; Mphale et al., 2014; Cahill et al., 2013; Schmiedel et al., 2021). Changes in resource availability may impact the community structure of ecosystems, altering abundance and distribution of species (Munson et al., 2012). Hence, conservation of species that provide ecosystem services that help to maintain these resources is of great importance. However, the contribution of rare species (defined in my study as those occurring at low densities within suitable habitats) to the functionality of the ecosystem is often less understood or documented, which may lower their prioritisation in conservation efforts (Lyons et al., 2005). Despite the limited understanding of their ecological role, conservation efforts continue to prioritise rare species.

The contribution of rare species to ecosystem resilience is generally acknowledged, as they enhance an ecosystem's adaptability to changing conditions through their contribution to overall biodiversity and genetic diversity (Longton and Hedderson, 2000). However, it is often assumed that rare species have little influence on overall ecosystem functionality, apart from their existence and cultural value, or value as specialists, due to the lesser size of their populations and often small home ranges (Ingram et al., 2012). Yet, these rare species are often the most in need of conservation efforts, ultimately resulting in contradicting conservation objectives. Further research is required to understand if rare species contribute more to ecosystem functionality than their low densities and small home ranges suggest, so that conservation objectives can coincide with one another and incentivize management bodies to implement conservation strategies that account for the ecosystem services provided by rare and threatened species. Additionally, in order to classify the conservation status of species effectively, empirical data on both the threats faced by the species, and the value of the ecosystem services they provide, is required.

Specialist animals that provide a wide host of ecosystem services are fossorial and semi-fossorial mammals, which are adapted for digging and living predominantly underground. The burrowing and digging activities of Australian mammals for foraging and/or shelter, as an example, contribute to ecosystem services in the form of soil turnover, increases in local biodiversity and nutrient cycling (Fleming et al., 2013). Digging behaviour increases soil turnover, which in turn can result in alterations in the chemical and structural make-up of soils (James et al., 2009). These alterations can lead to improved nutrient cycling in the environment, increasing the availability of nutrients to other users in the system (Whitford and Kay, 1999). Digging allows for the accumulation of macro- and micro-organisms, such as fungi, invertebrates, and seeds (Martin, 2003). This accumulation of organisms can increase soil nutrient concentrations, seed germination and plant recruitment, ultimately leading to elevated levels of biodiversity (Ceballos, 1999). Furthermore, hydrological aspects of the environment are also influenced by dig sites through increased water infiltration, decreased surface run-off, and the retention of soil moisture, resulting in an increase in the water and nutrient availability for plants and animals (Bond, 1964; Fleming et al., 2013; Dundas et al., 2022). All of these processes are crucial to the functionality of an ecosystem, and so the role of fossorial animals is an important field of research.

One such fossorial animal is Temminck's pangolin, a nocturnal mammal and specialist feeder, found in varying habitats across eastern and southern areas of sub-Saharan Africa, and existing at low population densities (Challender et al., 2020; Pietersen et al., 2020). The IUCN has classified Temminck's pangolins as Vulnerable due to their decreasing population trend, largely as a result of their exploitation in the illegal wildlife trade (Pietersen et al., 2019a; Challender et al., 2020). Temminck's pangolins are recognised globally as a threatened mammal requiring urgent protection (Pietersen et al., 2019a). Despite their threatened status, the consequences of their loss in terms of ecosystem services are poorly understood. Gaining insights into their specific ecosystem services may allow for better alignment of conservation efforts to protect this vulnerable species and preserve their potentially important role within their ecosystem. My introductory chapter reviews the current literature on pangolins to identify gaps in the research and describes the foraging behaviour and ecosystem services of other fossorial animals in a dryland ecosystem.

1.1 Ecosystem services of fossorial mammals

In addition to their role in soil turnover, biodiversity accumulation, and nutrient cycling (Figure 1), fossorial and semi-fossorial animals provide ecosystem services by engaging in commensal relationships with other animals (Taylor and Skinner, 2001) and serving as prey for various predators (Beca et al., 2022). Species can affect the community structure of an ecosystem directly through trophic effects, or indirectly through alterations to the environment, affecting community composition (Sun et al., 2021; Fleming et al., 2013). The majority of ecosystem services that fossorial and semi-fossorial animals provide are as a result of bioturbation, where they alter and mix soils through their digging and foraging activities (Beca et al., 2022). Digging and burrowing actions can result in changes to habitat geography, allowing for habitat heterogeneity and the creation of microhabitats (Sun et al., 2021). Burrows created by fossorial and semi-fossorial animals are often utilised by other species as refuges from environmental stressors, such as fire, predation and air temperature fluctuations (Kinlaw, 1999). For example, aardvark (*Orycteropus afer*) and springhare (*Pedetes capensis*) burrows are utilised by at least 20 and 7 different species, respectively (Smithers, 1971). The burrows of Chinese pangolin have been recorded to be used by 14 mammal species, 17 bird, 4 reptile and 2 invertebrate species, highlighting these burrows as centres of ecological activity (Sun et al., 2021). Additionally, many species tend to shift their foraging behaviour in response to prey abundance, which itself is often influenced by local climatic variables (Baylis et al., 2008; Palmer and Woinarski, 1999; Lindsey and Skinner, 2001; Goundie et al., 2015). As such, the extent to which an animal impacts its environment may also vary seasonally.

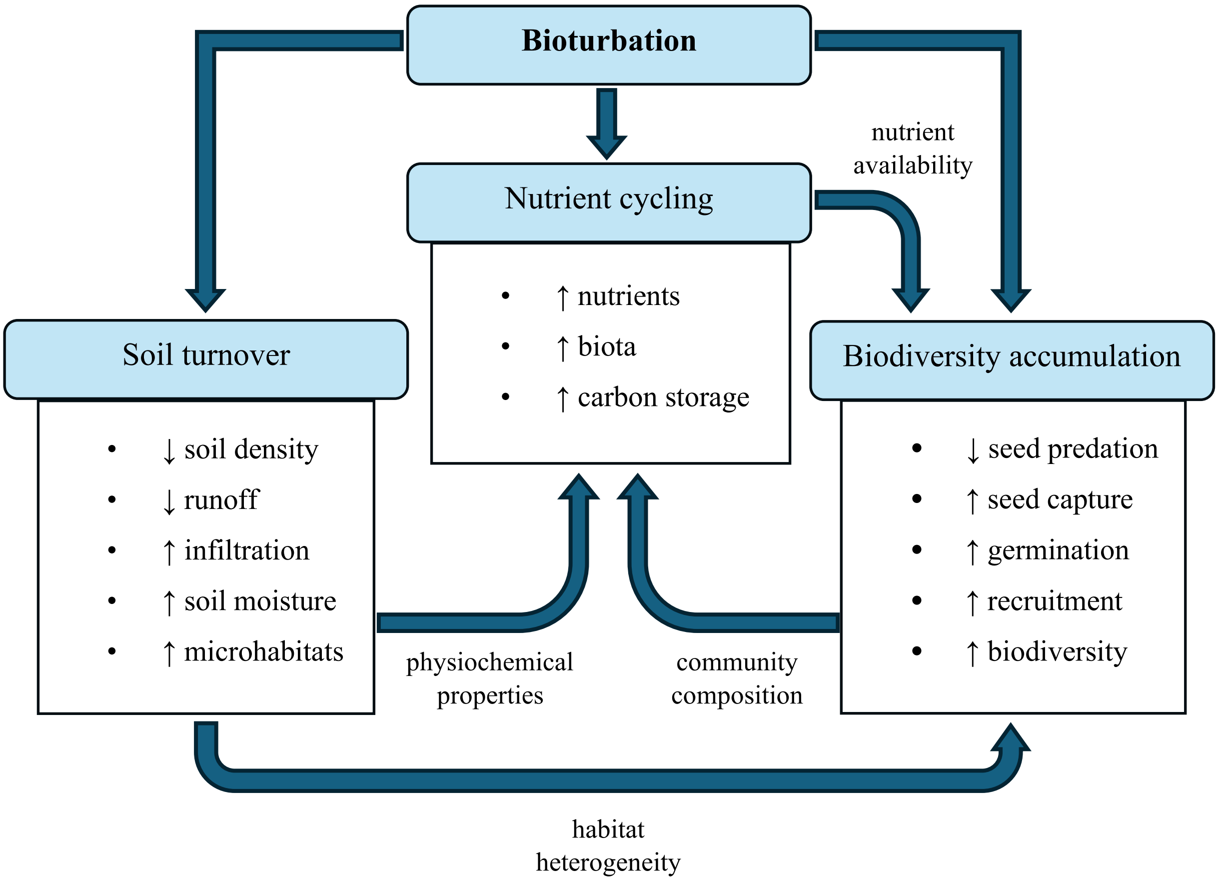


Figure 1. Flow diagram showing three main ecosystem services provided by fossorial and semi-fossorial mammals (adapted from Fleming et al., 2013; Beca et al., 2022; Sun et al., 2021; Kinlaw, 1999; James et al., 2009; Bond, 1964; Hagenah and Bennett, 2012; Martin, 2003; Radnan and Eldridge, 2017; Alkon, 1999). ↑ arrows indicate an increase and ↓ arrows a decrease.

Whilst the ecological role of some fossorial species, such as the echidna (*Tachyglossus aculeatus*) and porcupine (*Hystric africaeaustralis*), have been researched (Dundas et al., 2022; Alkon, 1999), there is little literature on the ecosystem services that pangolins provide, particularly Temminck's pangolins, through their foraging behaviours. The various behaviours and services provided by fossorial animals play an important role in shaping and maintaining ecosystems. Therefore, the loss of specific fossorial species may have cascading ecological consequences, emphasizing the need for more targeted conservation strategies. A total of 869 mammalian bioturbator (digging) species exist, of which 16 % are classified as threatened by the IUCN and 8 % are data deficient (Beca et al., 2022). Further loss of these species will mean the loss of crucial ecosystem services they provide, diminishing the functionality of ecosystems. Therefore, further research on the role of bioturbator animals, such as fossorial and semi-fossorial species, and their ecological contributions is necessary.

1.1.1 Soil turnover

In the context of my study, soil turnover refers to the mixing and redistribution of soil through animal foraging, digging and burrowing behaviours (Fleming et al., 2013; Sun et al., 2021). In addition to altering soil structural and chemical properties, digging behaviour of fossorial animals can influence hydrological aspects of the environment, through increased water infiltration, decreased surface run-off and the retention of soil moisture (James et al., 2009; Fleming et al., 2013; Figure 1). Previous research has found that fresh foraging activities of Chinese pangolins increase infiltration as digging behaviour increases soil permeability by penetrating the topsoil layer (Sun et al., 2021). The retention of soil moisture can increase water availability to plants and animals (Bond, 1964). Excavated soil creates patches of bare ground that may promote plant community succession, as a result of soil mounds burying old plants (Sun et al., 2021). These changes to the soil composition and landscape, propelled by the digging and foraging behaviours of fossorial animals, play a crucial role in maintaining ecosystems.

1.1.2 Biodiversity accumulation

For the purpose of my study, biodiversity accumulation refers to an increase in the species richness or the accumulation of organic material in a given area, through processes such as recruitment, succession, deposition, aggregation or seed capture (Rafferty, 2023; Fleming et al., 2013; Sun et al., 2021). Fossorial animals can play an important role in biodiversity accumulation through their digging and foraging activities. For example, seed aggregation can occur in dig holes, where seeds are less likely to be removed due to wind (Beca et al., 2022). Over time, these holes fill up and the seeds become buried (Beca et al., 2022). A change in community structure may occur as dig sites may provide microhabitats for organisms, promoted by elevated soil nutrients resulting from the decomposition of organic material (Sun et al., 2021). Microhabitat conditions may enhance seed germination and plant growth, while dig holes provide protection against predation (Radnan and Eldridge, 2017). Changes in the distribution and diversity of plant species can alter the distribution of food items and in turn attract herbivores, a large proportion of which are invertebrate species (Sun et al., 2021). Dig sites may also create seed banks, acting as a seed source for years after being dug (Beca et al., 2022). The foraging sites of Indian crested porcupines (*Hystrix indica*) promote seed germination and plant growth, by providing a more nutrient rich microhabitat as compared to undisturbed soil (Alkon, 1999). Dig sites can therefore pay a critical role in the concentration and increase of biodiversity within ecosystems. Examining the role of the dig sites of fossorial and semi-fossorial animals on biodiversity accumulation could therefore provide further insight into the importance of these animals and their roles within the environment.

1.1.3 Nutrient cycling

Nutrient cycling refers to the process whereby nutrients are moved and reused within the environment and is often facilitated through animal activity, such as bioturbation (Fleming et al., 2013). Fossorial and semi-fossorial animals can affect nutrient cycling in many ways, both directly and indirectly. Through their digging activity, fossorial animals bring deep soils up to the surface, increasing the nutrient availability for plants and animals (Bond, 1964). Digging can also cause organic matter to become buried, and together with increased soil moisture as a result of hydrological effects, can promote microbial activity (Sun et al., 2021). Increased microbial activity in turn increases the decomposition of organic matter, altering soil nutrients (Kinlaw, 1999). The burying of organic matter can also increase carbon storage within the environment (Beca et al., 2022). Furthermore, urination and defaecation by fossorial and semi-fossorial animals increase soil nitrogen and phosphorus concentrations (Beca et al., 2022; Dean and Milton, 1991b). It is speculated that fossorial species, such as armadillos (order Cingulata), ingest substantial amounts of soil during foraging, which may facilitate the translocation of nutrients in the environment through defaecation (Rodrigues et al., 2020). A study in the Cape Fynbos biome, South Africa, showed that the dig mounds of common mole rats (*Cryptomys hottentottus*) and the Cape mole rat (*Georychus capensis*) had higher nutrient concentrations (nitrogen and magnesium) than undisturbed soils, changing plant species composition (more grasses and legumes) and enhancing plant species richness (Hagenah and Bennett, 2012). The extent to which the activities of fossorial and semi-fossorial animals influence nutrient cycling is not yet clear. Therefore, further research is needed to quantify the impact of digging and foraging behaviours of species on nutrient cycling in order to understand their role within the ecosystem.

1.2 Foraging in a Dryland Ecosystem: Kalahari

Dryland ecosystems are characterised by low and highly variably annual rainfall, as well as high evapotranspiration rates (Wale and Dejenie, 2013). Dryland ecosystems include deserts, semi-arid and arid regions (Feng and Fu, 2013; Wale and Dejenie, 2013). Species inhabiting dryland ecosystems generally face challenging conditions, most notably water scarcity and large temperature fluctuations, which have led to the adaptation of specialist foraging behaviours (Ward, 2016). Arid-adapted animals are often able to get the majority of their water requirements from the food they consume, preformed water, meaning that they can go substantial lengths of time without access to free-standing water (Cain et al., 2006). The aardvark is an example of a fossorial animal that gains all its water requirements from its myrmecophagous diet (ants and termites; Taylor and Skinner, 2004). Animals in arid environments generally face significant trade-offs in meeting their energy requirements, often requiring them to change their foraging behaviour (duration, frequency and/or distance; Pyke, 1984; Norberg, 1977; Levy et al., 2016). For example, animals may reduce foraging duration or cease foraging altogether during periods of increased physiological challenges (increased temperatures and water loss) to reduce overall physiological costs, rather than prioritise food intake (Levy et al., 2016).

In the Kalahari, southern Africa, which was where my study was conducted, average annual air temperature is projected to increase 3.5 to 4.5 °C and rainfall to decrease by 10 to 30 % (given a median projection under a high emissions scenario; A2 SRES scenario; Engelbrecht et al., 2015), as a result of climate change. These projected climatic changes are expected to place further stress on the plant and animal species of the Kalahari (Schmiedel et al., 2021; Kapuka and Hlásny, 2021). The Kalahari experiences wet summers followed by dry winters, with large fluctuations in rainfall and air temperatures (Tyson and Crimp, 1998; Tokura et al., 2018). Vegetation growth and productivity in the Kalahari is closely linked to seasonal and interannual rainfall (van Rooyen and van Rooyen, 1998; Tokura et al., 2018). Insect populations, which serve as an important food source for many species in the Kalahari, are closely linked to air temperature, rainfall and vegetation growth (Lindsey and Skinner, 2001; Nunes et al., 2011; Meloni et al., 2020). Insect abundance and activity generally increase with decreased rainfall and increased air temperature, becoming more active and available to predator species (Fischer et al., 2022; Farji-Brener et al., 2018; Lindsey and Skinner, 2001; Jayatilaka et al., 2011). In some cases, increases in insect abundance during the rainy season (summer) are likely as a result of new vegetation growth, which often serves as the primary food source for harvesting insects (Fischer et al., 2022). Therefore, assessing the impact that climatic changes have on animals, both directly or indirectly through its effect on prey abundance, is critical to understanding how animals may shift and adapt their foraging behaviour in order to survive in dryland ecosystems.

1.3 Pangolins

1.3.1 General information

There are eight pangolin species, which are the only extant species belonging to the order Pholidota (Challender et al., 2020; Table 1). Pangolins are mammals, commonly known for their brown keratin scales that cover their body, providing protection against predation (Pietersen et al., 2020). Of the extant pangolin species, four are Asian and four are African (Challender et al., 2020; Table 1). Pangolins are primarily nocturnal, with the exception of the predominantly diurnal, black-bellied pangolin (Challender et al., 2020; Table 1). They are also typically solitary animals, coming together only for the mating season and when females take care of their young (Pietersen et al., 2020). Pangolins spend the majority of their time sleeping in burrows, rocky caves and crevices, or holes in trees, generally emerging at night to forage (Challender et al., 2020; Jacobsen et al., 1991; Pietersen et al., 2014b). Pangolins inhabit a diverse range of ecosystems, from subtropical forests (Chinese pangolin) to arid savannas (Temminck's pangolin; Challender et al., 2020; Table 1). Some pangolin species, such as the Chinese, giant and Temminck's pangolins, are fossorial, whilst the Indian, Sunda and Philippine and white-bellied pangolins are semi-arboreal, and the black-bellied pangolin is exclusively arboreal (Challender et al., 2020). Body mass also varies substantially between the eight species, ranging from 1 kg for the smallest species, the black-bellied pangolin, to 30 kg for the largest, the giant pangolin (Challender et al., 2020; Table 1).

Table 1. The location, activity period, body mass and conservation status of extant pangolin species (Challender et al., 2020).

Species	**Location**	**Activity period**	**Body mass (kg)**	**Conservation status**
Chinese pangolin (*Manis pentadactyla*)	Southeast Asia	Nocturnal	3 to 5	Critically Endangered
Indian pangolin (*Manis crassicaudata*)	South Asia, Indian sub-continent	Nocturnal	8 to 16	Endangered
Sunda pangolin (*Manis javanica*)	Southeast Asia	Nocturnal	4 to 7	Critically Endangered
Philippine pangolin (*Manis culionensis*)	Palawan faunal region in the Philippines	Nocturnal	4 to 7	Critically Endangered
Giant pangolin (*Smutsia gigantea*)	Equatorial Africa	Nocturnal	30 to 40	Endangered
Black-bellied pangolin (*Phataginus tetradactyla*)	West and central Africa	Diurnal	1 to 4	Vulnerable
White-bellied pangolin (*Phataginus tricuspis*)	West and central Africa	Nocturnal	1 to 3	Endangered
Temminck's pangolin (*Smutsia temminckii*)	East and southern Africa	Nocturnal	6 to 10	Vulnerable

1.3.2 Conservation status

Pangolin species have varying conservation statuses, with three species being listed as Critically Endangered on the IUCN Red List of Threatened Species, three as Endangered, and two as Vulnerable (Challender et al., 2020; Schoppe et al., 2019; Mahmood et al., 2019; Nixon et al., 2019; Pietersen et al., 2019b; Ingram et al., 2019; Pietersen et al., 2019a; Table

1). Despite these varying classifications, the populations of all eight species are declining (IUCN, 2024). Their threatened status is largely due to overexploitation from both poaching (for bush meat) as well as the international illegal wildlife trade, which is showing an unprecedented demand for pangolin body parts for both luxury cuisine as well as traditional practices and medicines (Boakye et al., 2014; Boakye et al., 2016; Ingram et al., 2018). Other threats to pangolins include electrocution on electric fences, road mortalities, the destruction of their habitat and climate change (Pietersen et al., 2014a; Challender et al., 2020). Although pangolin trafficking and illegal trade has generally been limited to Asia, recent trends have shown its spread to parts of Africa, creating a largescale and global trade of African pangolin scales (Challender et al., 2020). This shift suggests that the Vulnerable status of African pangolin species may be at risk of changing to Endangered should this trend persist. In 2016 the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) uplifted the status of pangolins globally from trade appendix 2 to appendix 1, which affords them the maximum protection across the globe (Nash et al., 2018). Given their threatened status, pangolin conservation is critical, however their elusive and solitary behaviour has made studying wild populations challenging, leaving much unknown about pangolins globally (Pietersen et al., 2014a). Pangolin conservation efforts have largely been focused on international management, legislation and trade controls (Nash et al., 2018; Schoppe et al., 2019), as well as identifying and establishing conservation sites (Schoppe et al., 2019; Mahmood et al., 2019), while little work has been done to identify and promote the ecological role pangolins may provide.

1.3.3 Ecological role of pangolins

Despite the conservation status of pangolins, their ecological role is largely unresearched. Pangolins have a myrmecophagous diet, feeding almost exclusively on ants and termite species (Challender et al., 2020; Pietersen et al., 2016b). These insects function as important biological indicators of ecosystem health, through their contribution to fundamental ecosystem services such as nutrient cycling, seed dispersal and pollination (Chowdhury et al., 2023). Pangolins may therefore indirectly impact the ecosystem through their impact on trophic interactions, and their continued decline may have negative consequences for the ecosystem. All pangolin species, except for the black-bellied pangolin, perform digging activities for foraging of subsurface prey, and burrow creation or modification (Challender et al., 2020). The digging activities of Chinese pangolins influence soil turnover, water infiltration, soil runoff and erosion (Sun et al., 2021), whilst the contribution of digging activities by other pangolin species to the ecosystem remains unresearched. Furthermore, the foraging activities of pangolins may expose ants and termites, making them available to other species (Pieterson et al., 2020). While evidence suggest that pangolins may contribute to overall ecosystem functioning, research on the direct ecosystem services that they provide has been limited, with most research being focused on Asian pangolin species (Sun et al., 2021). The lack of literature on pangolin ecosystem services creates a challenge in assessing the ecological impact of pangolin loss, which in turn hinders effective management and conservation efforts. Further research is needed to ascertain the extent to which pangolins provide ecosystem services.

1.3.4 Temminck’s pangolin

Temminck’s pangolin is widely distributed across Africa, primarily in Southern and East Africa, with records of individuals as far north as Sudan and Chad (Pietersen et al., 2014b; Pietersen et al., 2019a; Pietersen et al., 2020). Temminck’s pangolin is the only pangolin species to occur in southern Africa (Pietersen et al., 2020), where my study was conducted (southern Kalahari, South Africa). Their distribution is largely determined by the abundance of suitable prey species, habitat quality, and burrow availability (Pietersen et al., 2016a). Temminck's pangolins will frequently utilise the burrows of other burrowing animals, such as aardvarks, cape porcupines or springhares (Challender et al., 2020; Pietersen et al., 2020; Figure 2). The species occurs in a wide range of environments but primarily inhabits semi-arid, mesic savanna and woodlands, and does not occur in closed-canopy forests or true deserts (Pietersen et al., 2014b; Pietersen et al., 2020). The average body mass for the species is 6 to10 kg (Table 1), while in north Africa a male individual of 21 kg has been recorded (Challender et al., 2020, Sweeney, 1974). In the Kalahari, pangolins have home ranges that span 6.5 km^2, with home ranges in arid environments typically being larger than that of high rainfall areas (~9.9 km^2), which tend to have higher resource availability (Alcalá-Galván and Krausman, 2013; Pietersen, 2013; Pietersen et al., 2014b). Population density estimates are hard to obtain due to a lack of research and difficulties in studying this elusive species (Pietersen et al., 2016a; Pietersen et al., 2014b; Pietersen et al., 2021). However, in South Africa, densities are estimated to be 0.23 to 0.31 individuals per km^2, with higher densities in arid regions (0.31 individuals per km^2) compared to the more mesic eastern region of the country (0.24 individuals per km^2; Pietersen et al., 2014b; Swart, 2013). These densities lead to a population estimate of 16 000 to 24 000 mature individuals in South Africa (Pietersen et al., 2016a).

Figure 2. Aardvark burrow utilised by a pangolin. Photo credit Daniel Rossouw.

As a specialist feeder, Temminck's pangolins have a host of adaptations for feeding on ants and termites, including a strong sense of smell, a long sticky tongue, and powerful clawed forelimbs for digging open subterranean ant and termite nests, above-ground termite mounds and ant nests under bark (Pietersen et al., 2020; Swart, 2013; Swart et al., 1999). Temminck's pangolins tend to dig shallow holes, less than 20 cm deep, to access a single prey species colony, with feeding bouts lasting around 40 seconds (Swart et al., 1999). It is likely that the duration of feeding bouts is limited by the chemical and physical defences employed by ants and termites (Swart et al., 1999). It is estimated that individuals spend approximately 16 % of their active phase foraging (Swart et al., 1999). Pangolins obtain all the water they require from their prey; however, they have been known to drink free-standing water if it is available

(Pietersen et al., 2020). In the Kalahari, Temminck's pangolins were observed to feed on three dominant prey genera, namely *Crematogaster* ants (mean ± standard deviation [SD]; 50.2 ± 24.3 % of their diet), *Anoplolepis* ants (31.2 ± 24.0 %) and *Trinervitermes* termites (11.9 ± 10.2 %; Panaino et al., 2022). Pangolin individuals have been estimated to consume on average 15 398 ± 5 814 ants and termites during a 24h period (Panaino, 2021)

Temminck's pangolins have been recorded to adjust their activity patterns in response to changes in resource availability (Panaino et al, 2022; Panaino, 2021). The mean ± SD duration of the 24h above-ground active phase of Temminck's pangolins in the Kalahari has been recorded as 6h16min ± 0h46min (ranging from 1h07min to 15h45min; Panaino, 2021; Supplementary Table 1). The mean active phase duration was longer during summer, 07h00min ± 02h00min, as compared to winter, 05h14min ± 01h25min (Panaino, 2021; Supplementary Table 1). True nocturnal activity, defined as both emergence from and return to a burrow occurring between 18:00 and 06:00, was observed 48 % of the time, while truly diurnal activity, occurring between 06:00 and 18:00, was only recorded 2 % of the time, predominantly during winter (Panaino, 2021). It was shown that seasonal variation in the duration of the active phases of pangolins was related to environmental temperatures, photoperiod (day length) and pangolin 24h minimum body temperature (Panaino, 2021). The duration of the active phase of pangolins was shorter during winter, when environmental temperatures were decreased, and day length was short (Panaino, 2021). The timing of pangolin activity (emergence from and return to burrow times) was associated with prey abundance, with the active phase of pangolins starting and ending earlier when prey abundance decreased (Panaino, 2021).

1.3 Problem statement

Despite Temminck's pangolins being the most well-researched pangolin species in Africa, with extensive literature on the threats they face, little research has examined their ecological role and what losing the species (through illegal poaching, for example) may entail for the functionality of the ecosystem (Challender et al., 2020, Heath and Coulson, 1997; Swart et al., 1999; Pietersen et al., 2014b; Panaino et al., 2022). Based on studies of other pangolin species, such as the Chinese pangolin, it has been suggested that the Temminck's pangolin may impact its ecosystem through its role in nutrient cycling, soil turnover, insect population control and the accumulation of biodiversity in dig sites (Challender et al., 2020; Sun et al., 2021). However, this impact remains largely unexplored due to the lack of empirical data to support these claims. My study aims to address this gap in the literature by examining the ecological role of the Temminck's pangolin in the environment through quantifying the ecosystem services that they provide in a dryland environment which will, in turn, allow for the mobilisation and prioritisation of conservation efforts for this rare and vulnerable species.

1.4 Aims and objectives

The broad aims of my study are to (a) gain an understanding of Temminck's pangolin foraging behaviour and patterns (foraging frequency and distance foraged) in relation to seasonal prey abundance, with consideration of climatic factors, and (b) evaluate the ecosystem services pangolins provide through their foraging activities.

Objectives and hypotheses for aim a:

1. To determine the seasonal frequency of foraging sites created and the distance travelled by pangolins during foraging activities.

I hypothesised that the foraging frequency of pangolins will vary seasonally, increasing in winter and decreasing in summer in response to changes in prey abundance. Additionally, the distance covered by pangolins during foraging will also vary seasonally, with a larger distance covered during winter as compared to summer.

2. To quantify the seasonal abundance of pangolin prey within the environment.

The prey abundance of pangolins will vary seasonally, increasing in summer and decreasing in winter, as a result of seasonal climatic factors.

Objectives and hypotheses for aim b:

3. To measure the seasonal soil turnover generated by pangolin foraging activities.

Soil turnover generated by pangolins is hypothesised to vary seasonally in relation to variations in prey abundance, increasing as prey abundance decreases.

4. To measure the biodiversity accumulated inside pangolin foraging digs.

Pangolin foraging digs will increase the biodiversity accumulated, concentrating organic matter within their foraging area across a year.

5. To quantify the nutrient cycling of soil carbon and nitrogen that occurs from pangolin digging activity.

Pangolin foraging behaviour will increase soil carbon and nitrogen concentration over time.

1.5 Structure of the dissertation

My dissertation consists of five chapters. Chapter 1 is a general introduction to the research topic, reviewing relevant literature on the ecosystem services of fossorial animals and providing general information on pangolins. Chapter 2 outlines general methodologies used in each of the subsequent results chapters. Chapter 3 investigates pangolin foraging behaviour and patterns (Aim a), and includes methodology, results and a discussion of the findings.

Chapter 4 evaluates the ecosystem services provided by pangolins through their foraging behaviour (Aim b), and includes methodology, results and a discussion of the findings. Chapter 5 provides a conclusion and summary of the findings, with a discussion of the practical implications of the findings.

CHAPTER 2

General methods and materials

2.1 Site description

My study site was the 114 000 ha Tswalu Kalahari Reserve, Northern Cape, South Africa (27.2445˚ S, 22.4051˚ E; Figure 3). The reserve falls within the species distribution of Temminck's pangolins, covering one of the natural habitats of the pangolins, that of a dryland savanna ecosystem. The western and central areas of the reserve are covered by sandy plains and dunes running adjacent to a rocky mountainous area in the east (Figure 4). The five major vegetation types across the reserve are Koranna-Langeberg Mountain Bushveld, Gordonia Duneveld, Gordonia Plains Shrubveld, Olifantshoek Plains Thornveld and Kathu Bushveld (Tokura et al., 2018). Pangolins have been observed across all areas and vegetation types of the reserve; however, the individuals monitored during my study mostly utilised the Gordonia Duneveld and Gordonia Plains Shrubveld vegetation areas. The air temperatures of the region range from a summer daytime maximum of 42.5 °C to a winter nighttime minimum of -6.6 °C, with an annual average air temperature of 21.1 °C during my study period (van Rooyen and van Rooyen, 2017; VitalWeather, https://vitalweather.co.za). The reserve receives highly variable rainfall, with an annual mean of 360 mm ± 170 mm, largely occurring during the wet summer period (December to February; Tokura et al., 2018). The wet summers are followed by dry winters (June to August), during which air temperature frequently drops below freezing (van Rooyen and van Rooyen, 2017). In the years prior to my study, the reserve experienced multiple years of above-average rainfall, with 580 mm recorded from July 2020 to June 2021 and 635 mm from July 2021 to June 2022. For my study, summer and winter were defined as above, with autumn defined as March to May and spring as September to November.

Figure 3. Satellite images of Tswalu Kalahari Reserve (red triangle), situated in the Northern Cape, South Africa.

Figure 4. Gordonia Duneveld (foreground) and Koranna-Langeberg Mountain Bushveld (background). Photo credit Daniel Rossouw.

Tswalu has both lion (*Panthera leo*; Lekgaba) and lion-free sections (Korannaberg), separated by electric fencing (Figure 5). My study was conducted in the lion-free portion of the reserve, where other predators such as cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*) and spotted hyena (*Crocuta crocuta*) are present. Aardvark, aardwolf (*Proteles cristata*) and bat-eared fox (*Otocyon megalotis*) are some of the myrmecophagous species, other than pangolins, that occur on the reserve.

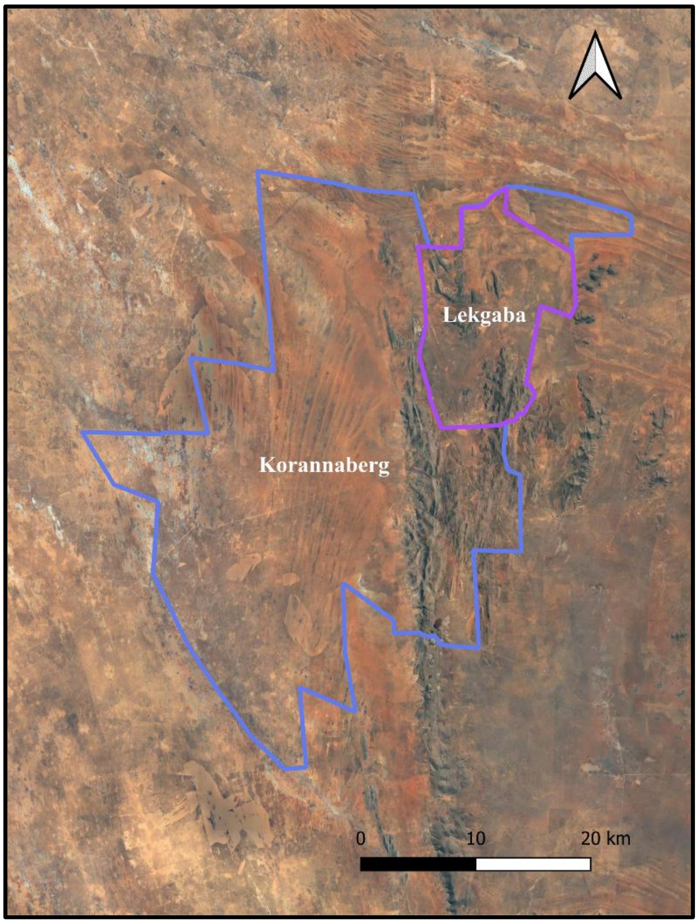


Figure 5. Satellite images of Tswalu Kalahari Reserve showing the boundaries of the reserve (blue) and Lekgaba (purple), separating the Korannaberg and Lekgaba sections.

2.2 Study animals and telemetry fitting

Four Temminck's pangolins were opportunistically located, and each was tagged with a VHF tracking transmitter (Africa Wildlife Tracking, Pretoria, South Africa, ~40 g) to allow me to locate them during their active phase (Figure 6a). Locating and tagging pangolins was performed with the assistance of staff and guides at Tswalu. The tag that was used weighed <1 % of the lower limit of pangolin body mass (6 kg) used in my study. When a pangolin was found it was moved into an open clearing, no more than 3 m away. The natural defence mechanism of a pangolin is to roll into a ball when threatened, making it easy to tag during the handling process. The tag was attached by drilling a single hole into a large dorsal scale at the base of the pangolin's tail (above the hind legs) and attaching it with a single 3 mm bolt

(Figure 6b). The process did not require anaesthesia of the animal, and the team undertaking the tagging had extensive experience in tagging pangolins. The hole was drilled into a non-vascularized section of the scale and a backing material (offcut of a tracking collar) was used underneath the scale, to avoid any potential injury to the animal. The tag was attached far enough from the edge of the scale so that it was not at the weaker tip of the scale, preventing any possibility of a scale breaking. Once tagged, the persons involved in the tagging process moved out of the area, allowing the pangolin to return to its normal, undisturbed behaviour. The individual was checked on the following day to make sure that there were no apparent ill effects from the procedure.

Figure 6. VHF tracking transmitter attached to the dorsal scale of a pangolin (a), and a close-up of the single attachment point of the tracking transmitter (b). Photo credits Daniel Rossouw.

Animals were tracked regularly (at least once a week) using telemetry (TR-8 handheld scanning receiver, range 138 to 235 MHz, Mesa, Arizona, United States of America and three-element folding Yagi antenna, range 145 to 155 MHz, Lotek Wireless Inc., Newmarket, Ontario, Canada), so that they could be located for observational purposes. The tracking was alternated between individuals as required throughout the year and across seasons. Alternating between individuals limited any continuous disturbance on any one individual, while alternating sampling methods ensured that sampling methods were spread across various conditions (time of day and climatic condition). An attempt was made to distribute sampling efforts evenly between individuals, however individuals tagged at an earlier date and for a greater length of time had greater representation in the sampling (Table 2). Short sampling durations for some pangolins were as a consequence of pangolins being predated, dispersing, or inhabiting inaccessible areas of the reserve.

Table 2. The date and duration for which each pangolin individual was tagged, along with the sex of each individual.

Pangolin individual	Date tagged	Duration tagged	Sex
HPW04	25/05/2022	10 months	Female
MM01	27/03/2023	7 months	Male
WG01	09/06/2023	3 months	Female
RS01	28/12/2023	3 months	Male

2.3 Ethical clearance and research permits

Ethical clearance for my research was granted by the University of the Witwatersrand Animals Research Ethics Committee (AREC; AREC23-03-014B; Appendix A). The required permits, TN 2081/2022 and TN 2082/2022, were attained from the Northern Cape Department of Agriculture, Environment, Land Reform and Rural Development.

CHAPTER 3

Patterns of pangolin foraging behaviour in response to prey abundance

Abstract

Numerous studies have documented the role animals play in their environment through the ecosystem services that they provide. However, the extent of their ecosystem services may be dependent on their ecological behaviour and factors which may cause shifts in this behaviour, such as prey abundance. While there is extensive literature on the foraging behaviour of large mammals, and to some extent fossorial animals, little is known about the foraging behaviour and patterns of pangolins. Therefore, my study aimed to gain an understanding of Temminck's pangolin foraging behaviour and patterns, by determining seasonal frequency of foraging sites created and the distance travelled by pangolins during foraging activities, and how they may be affected by prey abundance. I tagged and tracked four pangolins using VHF telemetry to collect data on their foraging behaviours and used pitfall traps to measure monthly prey abundance (ants per trap). The mean foraging frequency of pangolins was 12.5 ± 7.3 sites per hour and varied seasonally, with peaks in summer (17.9 ± 4.4 sites per hour) and winter (14.4 ± 9.7 sites per hour) as compared to lower values in autumn (11.3 ± 6.3 sites per hour) and spring (8.5 ± 3.9 sites per hour). The mean distance foraged per hour, 0.2 ± 0.1 km, did not differ seasonally. Prey abundance showed seasonal variation, increasing in summer (28.7 ± 23.2 ants per trap) and autumn (27.0 ± 28.1 ants per trap) and decreasing in winter (13.7 ± 17.3 ants per trap) and spring (13.4 ± 13.1 ants per trap). Prey abundance was 115 % higher in summer as compared to in spring. Foraging frequency was not linked to prey abundance, however, the distance foraged was positively associated with prey abundance. The results of my study provide support for seasonal variability in pangolin foraging behaviour, and its potential link to prey abundance. It is predicted that dryland environments will continue to experience rising air temperatures and greater rainfall variability, as a

consequence of climate change. Changes in climatic conditions are likely to affect pangolin prey abundance, which may, in turn, alter pangolin foraging behaviour and impact their ecological role. However, the extent of this impact remains unclear.

3.1 Introduction

The various ways in which mammals alter their environment through activities such as foraging, digging, grazing, browsing, and trampling are well documented (Fleming et al., 2013; Maestre et al., 2022; Pascual et al., 2017). These activities are critical for the environment as they contribute to soil turnover, redistribution of nutrients, hydrological impacts, vegetation control, seed dispersal (James et al., 2009; Fleming et al., 2013; Kinlaw, 1999; Beca et al., 2022; Sun et al., 2021). Although less widely researched compared to large herbivores and predators, fossorial and semi-fossorial animals play a significant role in shaping their environment through their foraging activity. The burrowing and foraging behaviours of fossorial and semi-fossorial animals contribute to numerous ecosystem services (Fleming et al., 2013). However, in order to quantify the ecological role of animals, it is important to first understand their foraging behaviours and patterns.

Foraging behaviour refers to the methods by which animals obtain the food and nutrients they require to fulfil their energetic needs (Pyke, 1984; Breed and Moore, 2012). In order to understand the impact that foraging behaviours have on the ecosystem, it is important to consider and measure key parameters such as the quantity and type of food consumed, the duration and frequency of foraging events, as well as the distance that animals travel during foraging. Many species have been observed to shift their foraging behaviours across seasons, often in response to changes in prey abundance (Baylis et al., 2008; Palmer and Woinarski, 1999; Fleming and Heithaus, 1986). Prey abundance, in turn, is influenced by local climatic variables (Lindsey and Skinner, 2001; Pearce-Higgins et al., 2010; Jayatilaka et al., 2011; Garcia-Heras et al., 2017), which may directly or indirectly impact foraging behaviours (Caldow and Furness, 2000; Goundie et al., 2015). As such, the extent to which an animal impacts its environment may also vary seasonally. Some small mammals such as the common shrew (*Sorex araneus*), for example, increase their foraging frequency during winter due to a decrease in the abundance of energetically profitable prey species, driven by shifts in environmental conditions (Churchfield et al., 2012). As a result of this shift in prey abundance, these mammals need to feed more frequently on less energetically profitable prey species to meet their energetic requirements (Churchfield et al., 2012). Furthermore, the distances that animals travel during foraging tend to increase during times of food scarcity (Owen-Smith and Cain, 2007; Pope and Jha, 2018). Sable antelope (*Hippotragus niger*), a large mammalian herbivore, increase their foraging distance during the transition period between the dry and wet season, when food resources are limited (Pope and Jha, 2018). Shifts in the foraging behaviour of animals can also cause variability in the intensity and extent of the ecosystem services that they provide (Dupont et al., 2011; Bracis and Wirsing, 2021). For example, the foraging behaviour of Griffon vultures (*Gyps fulvus*) varies based on farming practices, which either concentrate livestock carcasses into feeding stations (promoting central place foraging) or leave carcasses scattered for vultures to forage randomly (Dupont et al., 2011). When vultures used feeding stations, the efficiency of their scavenging service improved, however, the ecosystem service that they provided to farmers varied seasonally in response to variations in livestock mortalities (Dupont et al., 2011). The foraging behaviour of animals can also be driven by seasonal metabolic requirements that are not directly linked to prey abundance. For example, thermoregulation when environmental temperatures are elevated, such as in summer, can increase the metabolic demands, leading animals to reduce foraging activities and instead prioritise shading-seeking behaviour (Fuller et al., 2016).

While there is extensive literature on the foraging behaviour of large mammals, and to some extent fossorial animals, little is known about the foraging behaviour and patterns of pangolins. Pangolins, in general, are one of the most poached and trafficked mammals globally, making pangolin conservation critically important, particularly in regions where pangolins may face additional challenges such as those associated with climate change (Pietersen et al., 2019a; Challender et al., 2020; Engelbrecht et al., 2015). One such region expected to be increasingly impacted by climate change is the Kalahari, a dryland ecosystem in southern Africa where Temminck's pangolins occur (Pietersen et al., 2020). In the Kalahari, where my study took place, Temminck's pangolins shift their activity patterns in response to resource availability (Pietersen et al., 2014b; Panaino et al, 2022; Panaino, 2021). Panaino (2021) found that Temminck's pangolins had a mean 24h above-ground activity time of 6h16min ± 0h46min, which varied seasonally, decreasing in winter when prey abundance decreased and increasing in summer when prey abundance increased. The mean activity time was ~1h45min shorter during winter as compared to summer (Panaino, 2021). During winter the predominantly nocturnal activity of pangolins shifts towards an increase in diurnal activity (Panaino, 2021; Pietersen et al., 2014b; Challender et al., 2020). This activity shift highlights a key relationship between prey abundance and foraging duration and suggests that the pangolin's ecological role may also shift seasonally. However, certain aspects of pangolin foraging behaviour, such as foraging frequency and foraging distance, and their relation to prey abundance are still unknown. Understanding the foraging behaviours and patterns of pangolins is important for assessing how these behaviours may function as ecosystem services.

In this chapter, I aimed to gain further understanding of pangolin foraging behaviour and patterns (foraging frequency and distance foraged) in relation to seasonal prey abundance, with additional consideration of how climatic factors influence prey abundance. I assessed Pangolin foraging behaviour and patterns by measuring the seasonal frequency of foraging sites created and the distance travelled by pangolins during foraging activities. I quantified the seasonal prey abundance of pangolins to assess trends in pangolin foraging behaviour. I expected the prey abundance of pangolins to vary seasonally in relation to seasonal climatic factors (rainfall and air temperature), with prey being most abundant in summer (associated with increased rainfall and increased air temperature) and least abundant in winter (associated with decreased rainfall and decreased air temperature). I hypothesised that the foraging frequency of pangolins will vary seasonally, increasing in winter when prey abundance decreases and decreasing in summer when prey abundance increases. Similarly, the distance covered by pangolins during foraging will also vary seasonally, with a larger distance covered during winter when prey abundance decreases as compared to summer when prey abundance increases. In other words, I hypothesised that pangolins would increase their foraging frequency and distance foraged during periods of decreased prey abundance (winter) as compared to periods of increased prey abundance (summer).

3.2 Methods

3.2.1 Field sampling

3.2.1.1 Foraging behaviour

For the observation of foraging behaviour, four pangolins were located using VHF telemetry during their active phase and observed with a headlamp from a distance of 5 to 15 m. A distance of 5 to 15 m and the use of a headlamp for behavioural observations has previously been shown to cause negligible interference to natural behaviour of the animal (Panaino et al., 2022). When an individual was located, the observation session began once the first foraging site was observed. I defined a foraging site as a single site where a pangolin actively dug and scratched away soil or tore at the bark of a tree to access prey (Challender et al., 2020; Figure 7). During observations, the location of each foraging site was recorded using a handheld Global Positioning System receiver (Garmin eTrex 20x, 2 to 3 m accuracy, Garmin Ltd., Olathe, Kansas, United States of America). The location of each foraging site was recorded for a minimum of one hour, with observation sessions typically lasting one to three hours or until the individual entered a burrow, ending the active phase. To ensure that sampling sessions were representative of the entire active phase of pangolins, observations were performed for the full duration of their active phase for most individuals, once per season, where possible. With the use of a field guide (Slingsby, 2017) and reference collection (Dedeben Research Centre), the prey genera at each foraging site were identified and recorded. Foraging observations were performed across all seasons, summer (December to February), autumn (March to May), winter (June to August) and spring (September to November). Foraging observations were conducted across 2023 and 2024, with winter and spring observations in 2023, summer in 2024 and autumn in both years.

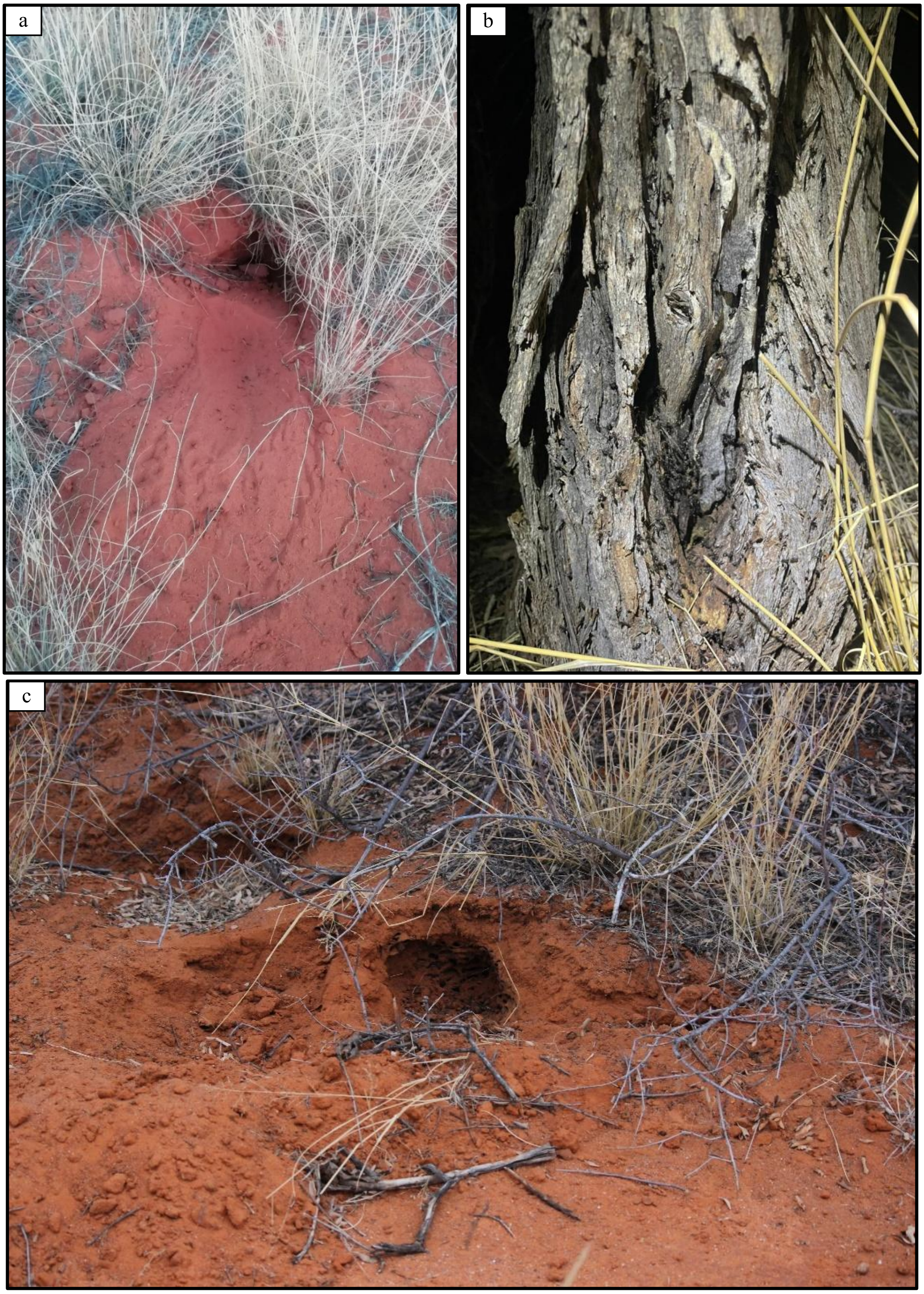


Figure 7. Pangolin foraging sites for *Anolpolepis* ants (a), *Crematogaster* ants (b) and *Trinervitermes* termites (c). Photo credits Daniel Rossouw.

3.2.1.2 Prey abundance

Prey abundance was recorded monthly over an 11-month period using pitfall traps (50 ml Falcon® Centrifuge Tubes, 27 mm diameter, Corning Inc., Massachusetts, USA; Figure 8). Thirty transects, each 50 m in length, were selected across the Korannaberg section of the reserve in areas where pangolins were known to occur. These transects form part of a larger data collection effort aimed at establishing a long-term dataset on prey abundance of the reserve (2015 to current). Transects were at least 500 m apart, and their orientation was randomly determined by tossing a stick and observing the direction in which it landed. Pitfall traps were placed five metres apart along each transects, with a total of 10 pitfall traps per transect, similar to methods used in previous research (Swart et al., 1999, Pietersen 2013, Panaino et al., 2022; Weyer, 2018). Traps were placed in the ground, with the opening of the trap level with the ground surface. Each tube contained 20 to 30 ml of antifreeze and water solution (100 ml commercial glycerol-based antifreeze: 1 L water). All traps were deployed for four days every month (four days of sampling). The number of ants that fell into the traps every month was counted and used as a proxy for prey abundance (Panaino, 2022; Swart et al. 1999; Pietersen, 2013). Termites were excluded due to low numbers recorded in traps (mean ± SD; 1.8 ± 4.9 %) and their minimal contribution to the pangolin's diet (4.0 ± 11.8 %; Panaino, 2022). All other insects, except ants, that fell into the traps were discarded and excluded from analyses.

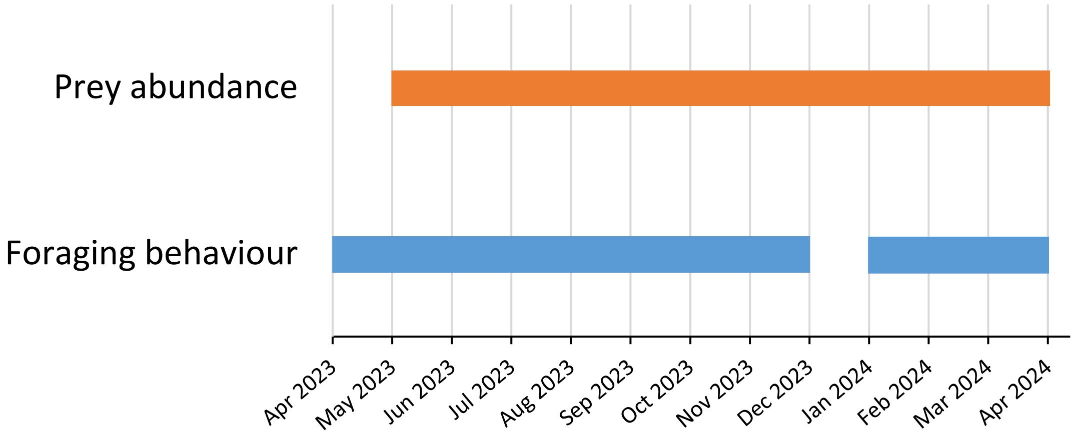


Figure 8. Timeline of the months during which prey abundance and foraging behaviour data were collected.

3.2.1.3 Climatic factors

Monthly average air temperature data were downloaded from a weather station (Vantage Pro2, Davis Instruments, Hayward, California, USA) based at the Tswalu airstrip on site (VitalWeather, https://vitalweather.co.za). Monthly rainfall data were obtained from Tswalu, where rain is measured using manual rain gauges. To account for the variability of rainfall across the reserve, I selected a gauge located centrally within the area covered by all study individuals.

3.2.2 Data analyses

All statistical analyses were performed using R (R Core Team, 2024), through the RStudio interface (v2023.6.1.524). A significance level of 0.05 was used. QGIS (version 3.38.3-Grenoble, QGIS Development Team, 2024) was used for the spatial analyses of pangolin foraging sites to investigate the space used during foraging activity. Convex hulls were used to estimate the cartesian area covered by pangolins during foraging observation sessions (foraging area), using the locations of their foraging sites. Furthermore, foraging density was calculated as the number of foraging sites per square kilometre, using the count of foraging sites divided by the foraging area for each observation session (foraging density = number of foraging sites/foraging area). When calculating the average foraging density, extreme outliers were removed using the Tukey's method (Q1 - 3 interquartile range [IQR], Q3 + 3 IQR) (Saleem et al., 2021), because during some of the short observation sessions (single hour) the area foraged was small (only two or three bushes), leading to abnormally high foraging densities.

3.2.2.1 Foraging behaviour

The analyses of pangolin foraging behaviour were separated into four main aspects, namely foraging frequency, distance foraged, the proportion of foraging sites associated with *Anoplolepis* ants and the proportion of foraging sites associated with *Crematogaster* ants (the two main ant prey genera). Foraging frequency was calculated as the average number foraging sites per hour, by dividing the count of observed foraging sites by the duration of the foraging observation for each observation session. Distance foraged was calculated as the average distance foraged per hour by applying the Haversine formula to determine the distance between consecutive foraging sites (Maria et al., 2020) and dividing the total distance between all foraging sites by the duration of the foraging observation for each observation session. The proportion of foraging sites associated with the two main prey genera was calculated for each observation session to assess whether pangolins changed their primary prey selection throughout the year. These four variables (foraging frequency, distance foraged, the proportion of foraging sites associated with *Anoplolepis* ants and the proportion of foraging sites associated with *Crematogaster* ants) made up the outcome variables. The predictor variables were season, prey abundance (ants per trap monthly average) and pangolin individual (random effect). However, due to a collinear relationship between season and prey abundance, separate models were run for season and prey abundance. Monthly averages of ants per trap were used as the measure for prey abundance because data were available at a monthly scale, aligning with the foraging behaviour data, which were also spread across months. Using monthly averaged prey abundance data provided greater variability, increasing the likelihood of detecting a relationship between foraging behaviour and prey abundance.

The analyses of pangolin foraging behaviour were conducted using linear mixed effect models (lme4 package; Bates et al, 2015). Linear mixed effect models utilise the residual maximum likelihood method to estimate parameters, and a t-test using Satterthwaite's approximation to test the significance of the fixed effects (Kuznetsova et al., 2017). Linear mixed effects models were used to assess each of the four outcome variables as a function of season and pangolin individual (as a random effect; Supplementary Table 2). Including pangolin individual as a random effect accounted for variability due to individual differences. Two additional linear mixed effects models were used to assess foraging frequency and distance foraged as a function of prey abundance and pangolin individual (Supplementary Table 2). The assumptions of linear mixed effects models were then checked. The model with foraging frequency as a function of prey abundance violated the model assumption of normality, hence a square-root transformation was applied to the foraging frequency (sqrt [foraging sites per hour]) improving the normality of residuals (Martin, 2021). For the model with distance foraged, pangolin individual was removed as a random effect due to insufficient variability, and a linear model was performed instead. The decision to use a linear model was supported by Akaike information criterion (AIC) values. The model with the lowest AIC value and a difference of more than three from the next best model was considered the best fit (Cavanaugh and Neath, 2019). AIC values indicated that the linear model provided the best fit (Supplementary Table 3). Furthermore, a model with foraging frequency as a function of distance foraged and pangolin individual (random effect) was run in order to examine the relationships between these two outcome variables (Supplementary Table 2). The model examining the relationship between foraging frequency and distance foraged violated the assumption of normality; therefore, a log transformation, with an added offset, was applied to both variables (log [foraging frequency or distance foraged + 1]). This improved the distributions of the positively skewed variables as well as the normality of residuals and ensured that all values remained non-zero and non-negative (Martin, 2021). Wald chi-square tests were used to assess whether the relationships between the predictor and outcome variables were significant. Furthermore, post-hoc Tukey's honestly significant difference (HSD) tests were performed to identify significant differences between seasons (emmeans package; Lenth, 2024).

Welch Two Sample t-tests were used to compare the foraging frequency and distance foraged between hourly foraging observation sessions and full active phase foraging observation sessions (base R; Supplementary Table 2). This was done to ensure that the hourly foraging observation sessions were an appropriate representation of the full active phase foraging observation sessions, and that foraging activity did not vary significantly throughout the active phase.

3.2.2.2 Prey abundance

A linear model was used to assess the seasonal variation in prey abundance (base R; Supplementary Table 2). The linear model assessed prey abundance (ants per trap) as a function of season, monthly rainfall (current, 2 and 3 months prior) and average monthly air temperature. Studies have shown that prey abundance is not necessarily influenced by the current month's rainfall but rather by rainfall two or three months prior (Panaino et al., 2022; van de Ven et al., 2020), hence the inclusion of various monthly rainfalls in the model. The assumptions of linear models were then checked. The model violated the assumption of normality; therefore, a log transformation, with an added offset, was applied to prey abundance (log [ants per trap + 1]). Additionally, extreme outliers were removed using the Tukey's method, as some prey abundance transects yielded abnormally high ants per trap counts. This improved the distributions of the positively skewed variable as well as the normality of residuals and ensured that all values remained non-zero and non-negative (Martin, 2021). However, the model still violated the assumptions of independent residuals and homoscedasticity. Therefore, a linear model using generalized least squares was run, using AR(1) as the autocorrelation structure and month as the variance structure (nlme package; Pinheiro et al., 2023; Supplementary Table 2). AIC values indicated that the model with only the current monthly rainfall was the best fit, hence rainfall for two- and three-months prior was removed (Supplementary Table 4). A Type II (marginal) analysis of deviance (ANOVA) tests were used to assess whether the relationships between the predictor variables and prey abundance were significant. Post-hoc Tukey's honestly significant difference tests were performed to identify where seasonal differences in prey abundance occurred (emmeans package; Lenth, 2024).

3.3 Results

3.3.1 Foraging behaviour

A total of 58 foraging observation sessions were performed (~98 hours), during which 1 258 pangolin foraging sites were recorded (Table 3; Table 4; Figure 9). Four full active phase observation sessions were performed, of which the second full active phase observation session for pangolin individual RS01 (autumn) had the highest number of foraging sites observed, 208 foraging sites, covering an area foraged of 3.1 km^2 (Figure 10). The mean ± SD foraging frequency was 12.5 ± 7.3 sites per hour and showed significant seasonal variation (n = 58, Wald, df = 3, $X^2 = 11.61$, $p < 0.01$**;** Figure 11; Supplementary Table 5; Supplementary Table 6). The pairwise comparisons, using the Tukey adjustment, showed no significant differences in seasonal foraging frequency (Supplementary Table 7). However, pairwise comparison performed without adjustment for multiple comparisons revealed a significant difference between seasons, with seasons of increased foraging frequencies (summer and winter) followed by decreased foraging frequency in the subsequent seasons (autumn and spring, respectively; Figure 11; Supplementary Table 8). While pairwise comparisons using the Tukey adjustment is common practice (Midway et al., 2020), unadjusted pairwise comparisons help retain sensitivity in detecting differences between seasons, particularly when the overall test of significance is close to the 0.05 or 0.01 thresholds (Keselman et al., 1999). The highest foraging frequency (17.9 ± 4.4 sites per hour) was observed in summer, while the lowest foraging frequency (8.5 ± 3.9 sites per hour) was observed during spring (Figure 11; Supplementary Table 5). The mean distance foraged per hour, 0.2 ± 0.1 km, did not vary significantly across seasons (n =58, Wald, df = 3, $X^2 = 5.90$, $p = 0.12$; Figure 12; Supplementary Table 5; Supplementary Table 6). The mean (± SD) foraging density was 32.8 ± 40.1 foraging sites ha^{-1}. Prey abundance was not a significant predictor of foraging frequency (n = 56, Wald, df = 1, $X^2 = 1.05$, $p = 0.31$; Supplementary Table 6), however, a positive relationship was found between distance foraged and prey abundance (n = 56, ANOVA, df = 1, F = 9.91, $p = 0.01$; Supplementary Table 9). There was a positive relationship between the log transformed foraging frequency and log transformed distance foraged (n= 58, Wald, df = 1, $X^2 = 15.16$, $p < 0.01$; Supplementary Table 6).

Table 3. The number of foraging observation sessions performed for different pangolin individuals, across different seasons.

Pangolin individual	**Foraging observation sessions**				**Total**
	Summer	**Autumn**	**Winter**	**Spring**	
HPW04	-	3	5	6 *	14
MM01	-	5	8	7 *	20
WG01	-	-	3	-	21
RS01	9 *	12 *	-	-	3
Total	9	20	16	13	58

*Full active phase observations occurred.

Table 4. The number of foraging sites for each pangolin individual, across different seasons.

Pangolin individual	**Foraging sites**				**Total**
	Summer	**Autumn**	**Winter**	**Spring**	
HPW04	-	16	52	182 *	250
MM01	-	62	124	83 *	269
WG01	-	-	59	-	59
RS01	234 *	446 *	-	-	680
Total	234	524	235	265	1 258

*Full active phase observations occurred.

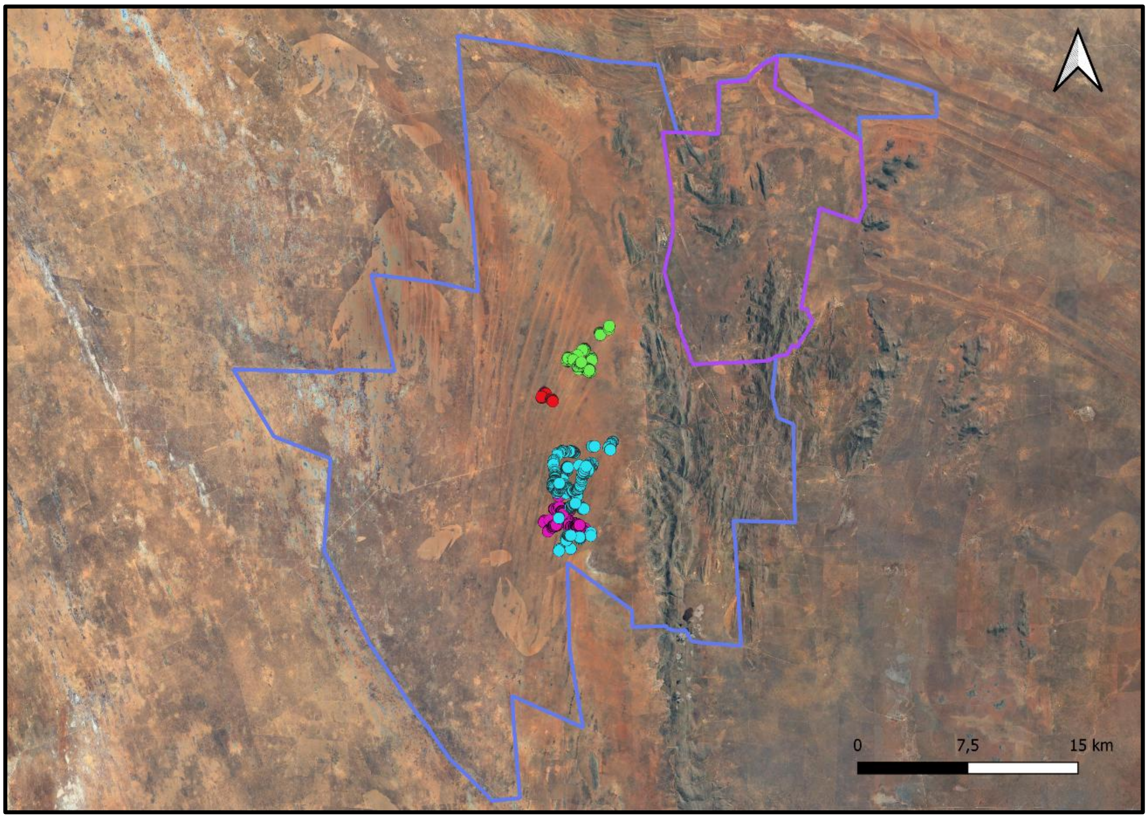
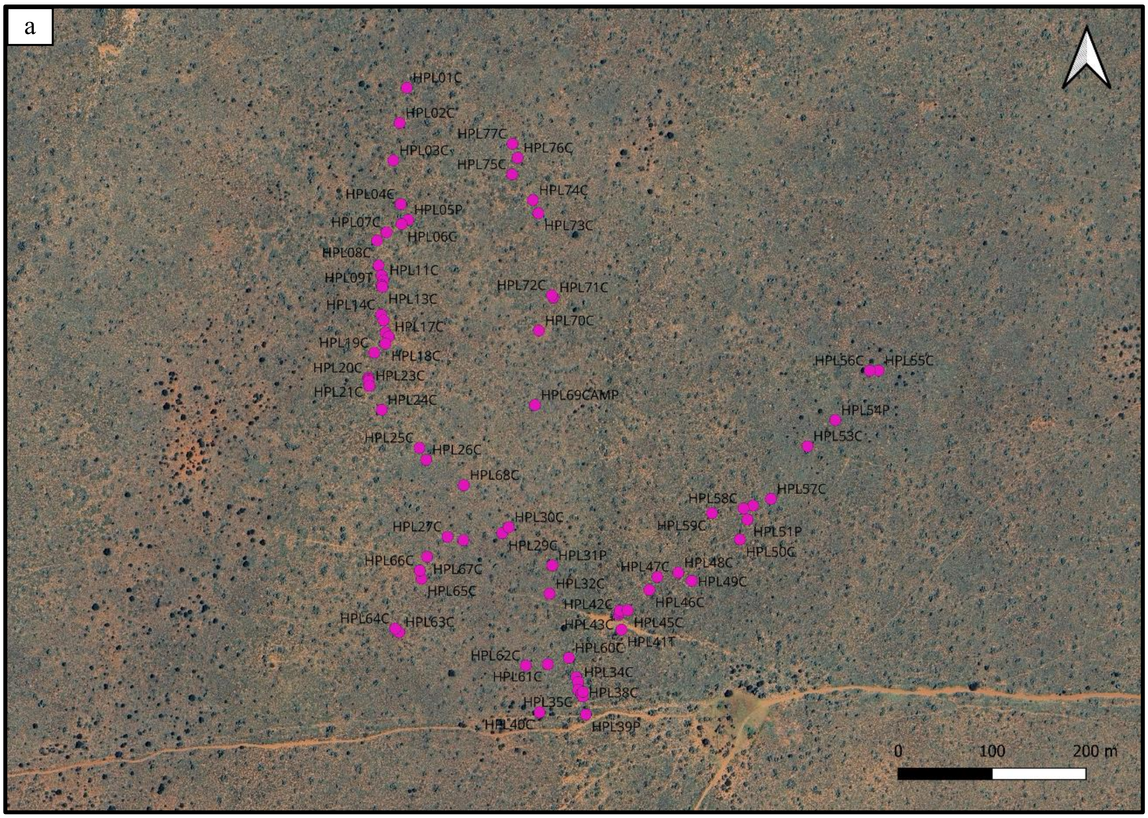


Figure 9. Satellite image of pangolin foraging sites recorded for each pangolin individual; HPW04 (pink), MM01 (green), WG01 (red) and RS01 (blue). Boundaries of the reserve (blue) and Lekgaba (purple) are shown.

a


HPL01C
HPL02C
HPL77C
HPL76C
HPL03C
HPL75C
HPL74C
HPL04C
HPL05P
HPL07C
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HPL06C
HPL08C
HPL09T
HPL11C
HPL72C
HPL71C
HPL13C
HPL14C
HPL17C
HPL70C
HPL19C
HPL18C
HPL56C
HPL55C
HPL20C
HPL23C
HPL21C
HPL24C
HPL69CAMP
HPL54P
HPL25C
HPL26C
HPL53C
HPL68C
HPL57C
HPL58C
HPL30C
HPL27C
HPL59C
HPL51P
HPL29C
HPL50C
HPL31P
HPL66C
HPL67C
HPL47C
HPL48C
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HPL32C
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HPL42C
HPL64C
HPL63C
HPL43C
HPL45C
HPL41T
HPL60C
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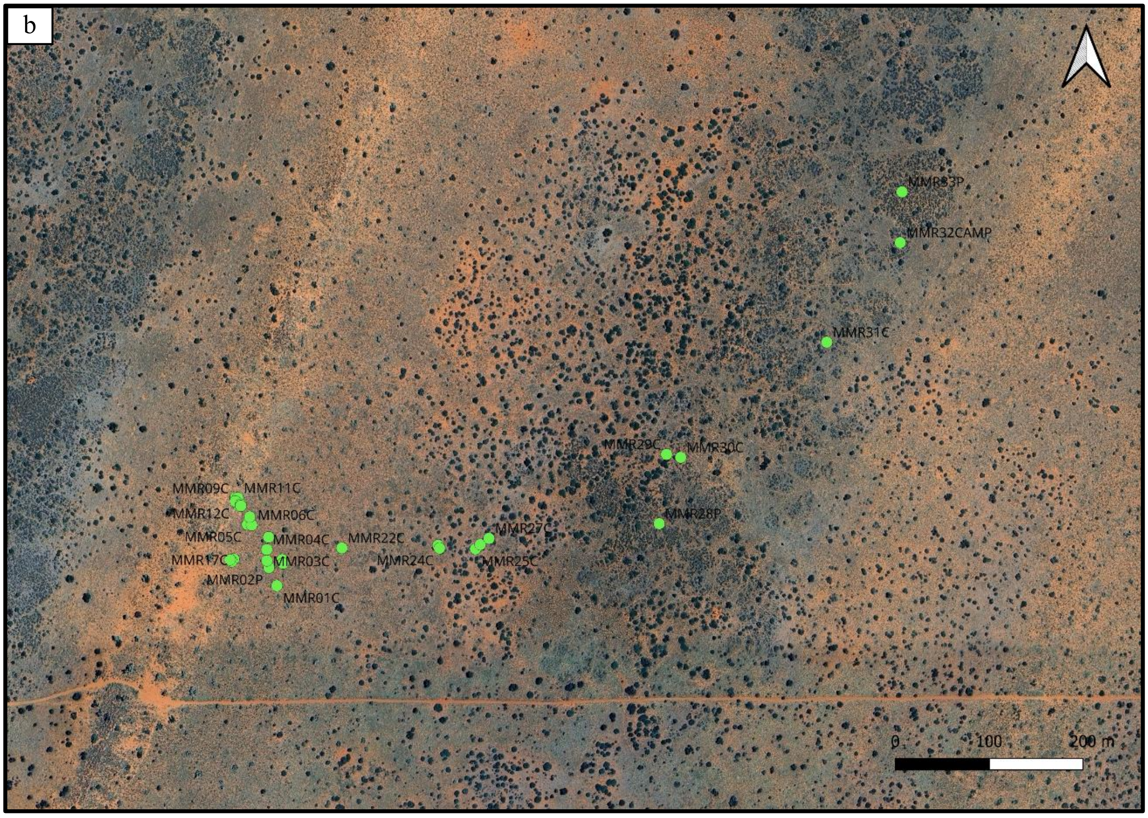
b


MMR33P
MMR32CAMP
MMR31C
MMR29C
MMR30C
MMR09C
MMR11C
MMR12C
MMR06C
MMR28P
MMR05C
MMR04C
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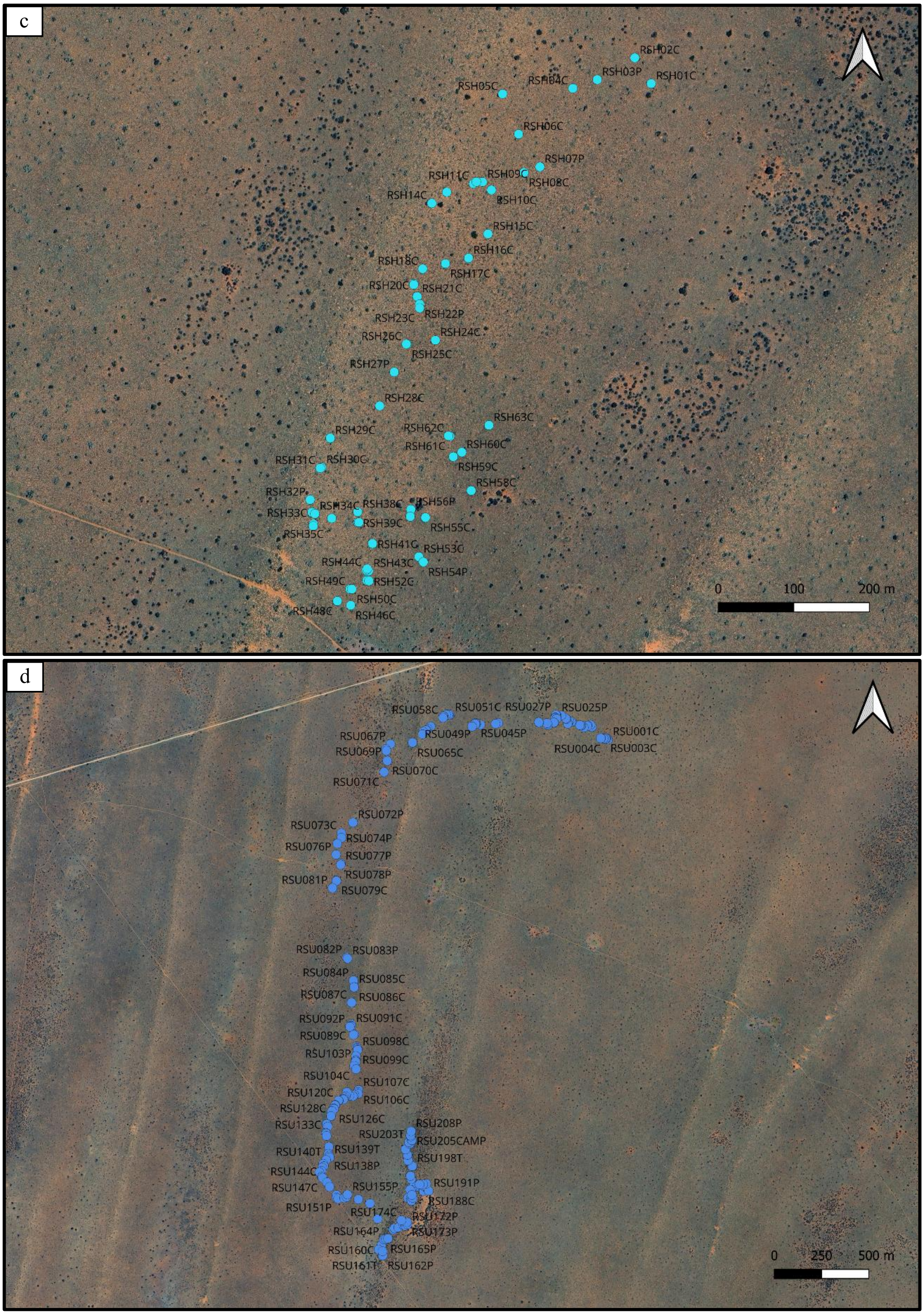

Figure 10. Satellite images of pangolin foraging sites recorded during full active phase observations for different individuals, HPW04 (spring; a), MM01 (spring; b), RS01's 1st full active phase (summer; c) and RS01's 2nd full active phase (autumn; d).

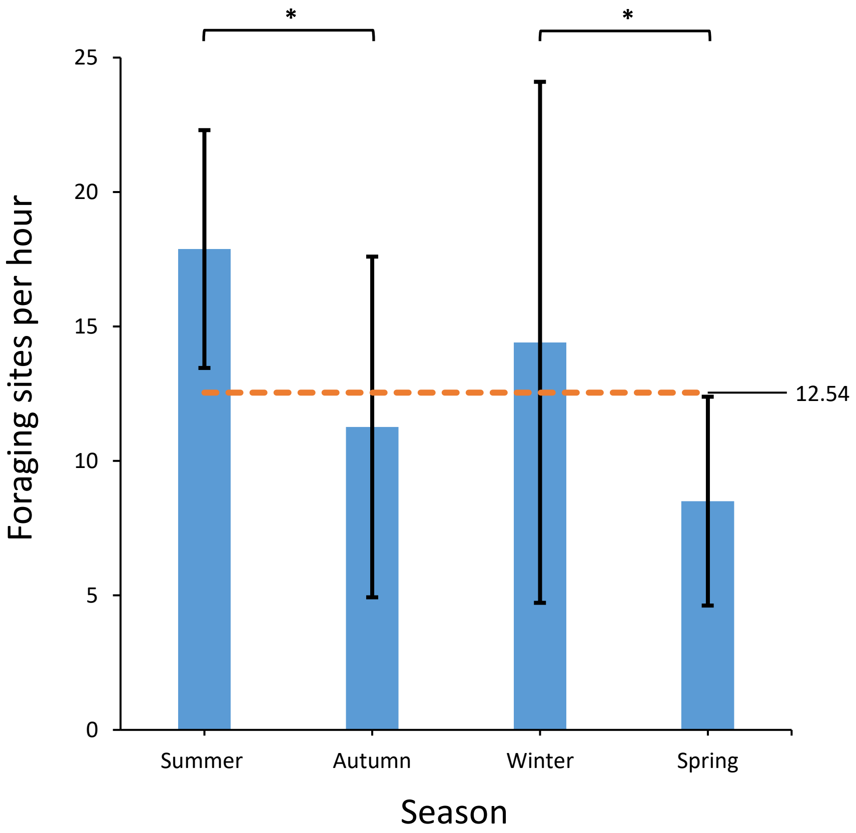

Figure 11. Mean pangolin foraging frequency (foraging sites per hour) across seasons. Error bars indicate standard deviation. The dashed orange line shows the mean pangolin foraging frequency across the year. Horizontal lines with asterisks indicate where pangolin foraging frequency differed between seasons at a significance level of 0.05 (without adjustment for multiple comparisons).

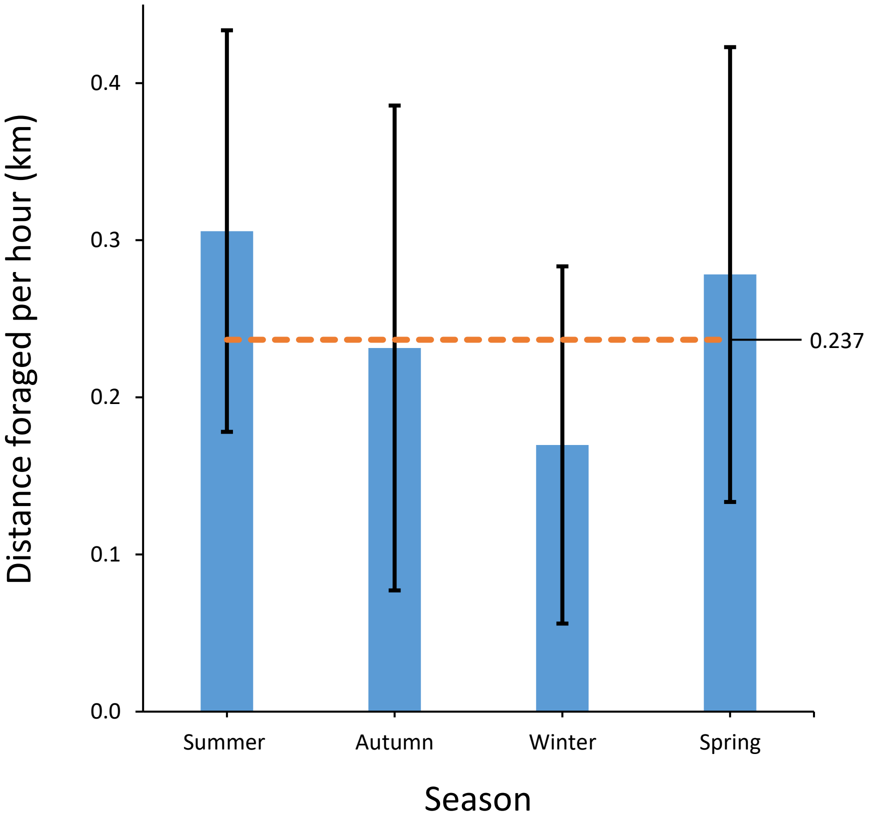

Figure 12. Mean pangolin distance foraged across seasons. Error bars indicate standard deviation. The dashed orange line shows the mean pangolin distance foraged across the year.

Four pangolin prey genera were recorded during foraging observations, with the majority of foraging sites being associated with *Crematogaster* ants (56.2 ± 35.1 %) and *Anoplolepis* ants (39.5 ± 35.7 %), and less frequently *Trinervitermes* termites (4.0 ± 11.8 %) and *Camponotus* ants (0.3 ± 1.1 %). There was significant seasonal variation in the proportion of pangolin foraging sites associated with the two main prey genera, *Crematogaster* ants (n = 58, Wald, df = 3, $X^2 = 33.70$, p <0.01) and *Anoplolepis* ants (n = 58, Wald, df = 3, $X^2 = 29.59$, p <0.01; Supplementary Table 6; Supplementary Table 7). The greatest proportion of foraging sites for all seasons was associated with *Crematogaster* ants, except during winter (25.2 ± 21.0 %), when *Anoplolepis* ants foraging sites made up the greatest proportion of foraging sites (66.7 ± 30.6; Figure 13).

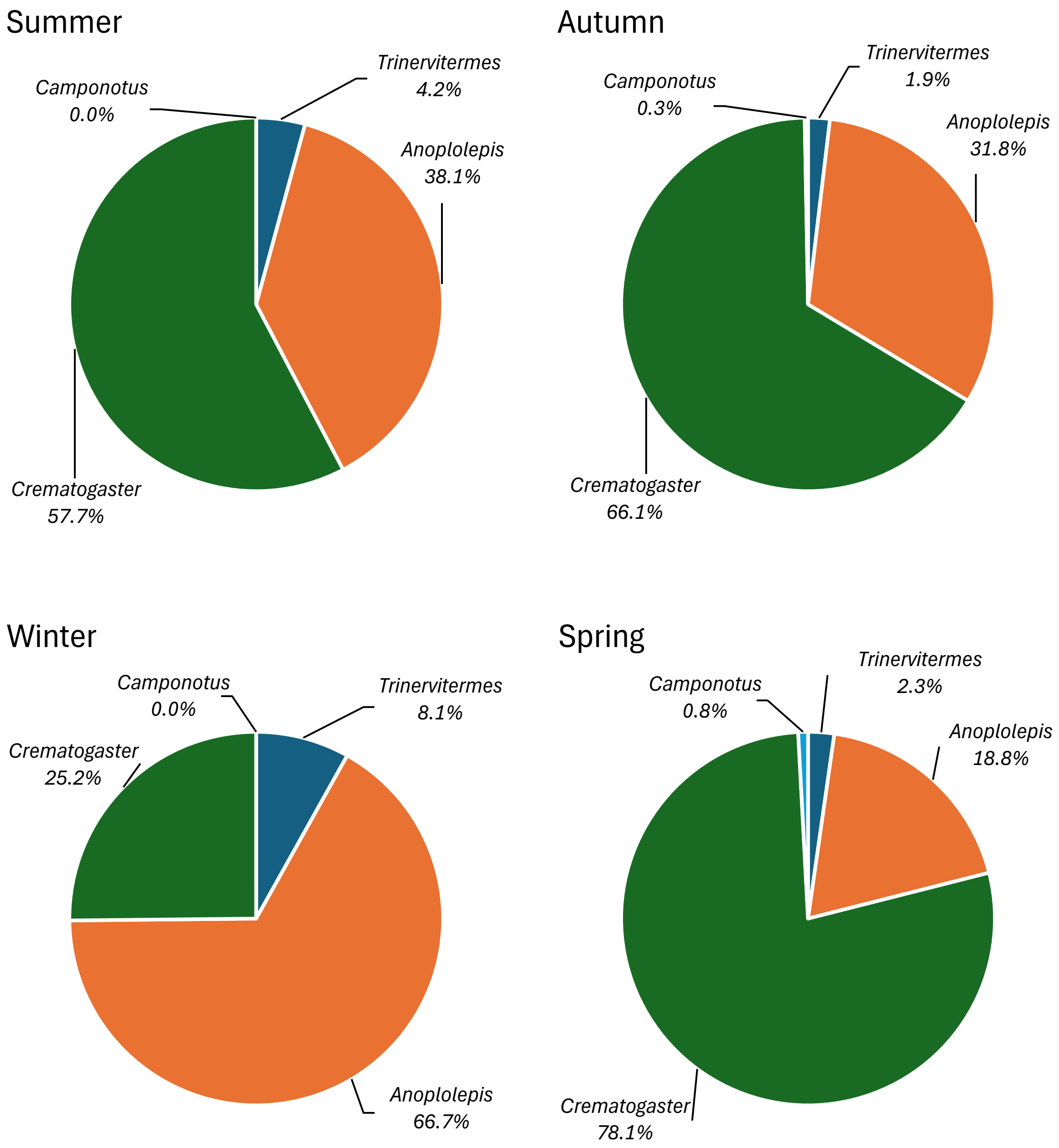

Figure 13. Seasonal proportion of pangolin foraging sites for each prey genera (*Crematogaster*, *Anoplolepis*, *Camponotus* ants and *Trinervitermes* termites).

There was no significant difference between the hourly (n = 54) and full active phase (n = 4) observation sessions for foraging frequency (Welch, df = 4.01, t = 0.19, p = 0.86) and foraging distance (Welch, df = 3.52, t = -2.07, p = 0.12). I was therefore confident that the hourly observation sessions were representative of the full active phase of pangolins.

3.3.2 Prey abundance

The linear model using generalized least squares showed that the log transformed prey abundance (ants per trap) varied significantly across seasons (n = 315, Wald, df = 3, X^2 = 35.62, p <0.01; Figure 14; Supplementary Table 9). The highest prey abundance (median and IQR) was recorded in summer (21.0 and 13.1 to 39.9 ants per trap) as compared to winter (6.7 and 3.2 to 16.9 ants per trap) and spring (9.5 and 4.4 to 17.4 ants per trap; Figure 14; Supplementary Table 10; Supplementary Table 11). The proportional abundance of *Anoplolepis* ants was highest in autumn (58.9 ± 31.8 %) and lowest in winter (10.5 ± 22.5 %), while *Crematogaster* ants was highest in spring (3.9 ± 8.2 %) and lowest in winter (<0.1 ± 0.1 %; Figure 15). There was a significant positive relationship between the log transformed prey abundance and average monthly air temperature (Wald, df = 1, X^2 = 40.94, p <0.01), while a significant negative relationship was observed between the log transformed prey abundance and monthly rainfall (Wald, df = 1, X^2 = 18.22, p <0.01; Supplementary Table 9).

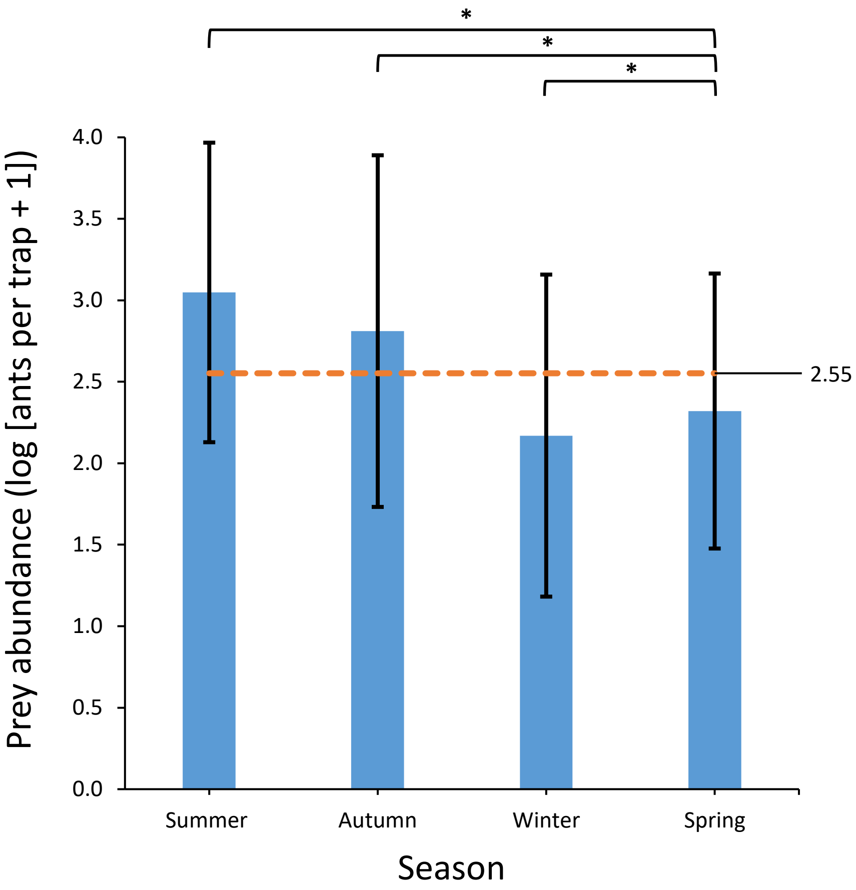

Figure 14. Mean logged pangolin prey abundance (log [ants per trap + 1]) across seasons. Error bars indicate standard deviation. The dashed orange line shows the mean logged pangolin prey abundance across the year. Horizontal lines with asterisks indicate where pangolin prey abundance differed between seasons at a significance level of 0.05 (Tukey adjustment).

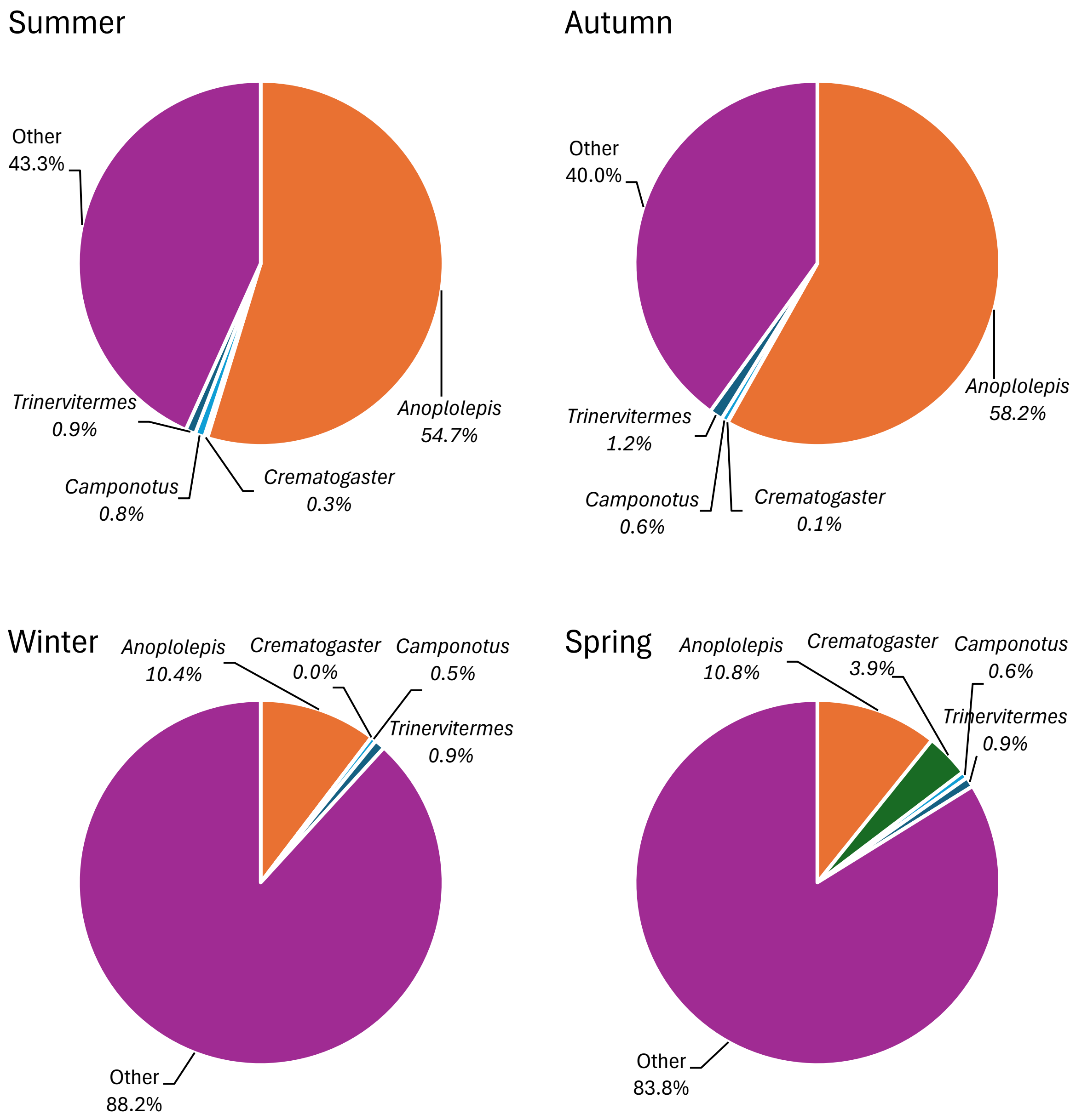

Figure 15. Seasonal proportion of prey abundance for the four major pangolin prey genera (*Crematogaster*, *Anoplolepis*, *Camponotus* ants and *Trinervitermes* termites) by season.

3.4 Discussion

The frequency of pangolin foraging changed seasonally, with peaks in summer and winter and declines in autumn and spring. Fluctuations in foraging frequency were not linked to seasonal variations in prey abundance. The seasonal variation in foraging frequency did not support the hypothesis that foraging frequency would increase in winter and decrease in summer in response to changes in prey abundance. Prey abundance increased in summer and autumn and decreased in winter and spring. There was no seasonal variation in the distance travelled by pangolins during foraging activities, but foraging distance was linked to prey abundance. Contrary to the original hypothesis, the distance travelled by pangolins during foraging was reduced during seasons of decreased prey abundance, whereas when prey was abundant, they travelled further. Seasonal variation in prey abundance was linked to seasonal climatic factors, supporting the initial hypothesis. Increases in prey abundance were linked to increases in air temperature and decreases in rainfall. The proportion of pangolin foraging sites associated with the two main prey genera (*Anoplolepis* ants and *Crematogaster* ants) varied seasonally, with *Crematogaster* ants being the dominant prey item throughout the year, except during winter where they were replaced by *Anoplolepis* ants as the dominant prey item.

Although attempts were made to address data limitations, such as accounting for pangolin individuals as a random effect in statistical models, certain constraints should be considered when interpreting the results. The largest limitation of my study was the small number of pangolin individuals, coupled with the fact that data was not collected across all seasons for any of the pangolin individuals. For some pangolin individuals, large portions of data were only collected during one or two seasons due to factors such as predation, dispersal, or individuals inhabiting inaccessible areas of the reserve. This lack of data severely limited interpretation of the random effect that pangolin individual may have had on the results, making it difficult to separate seasonal effects from variations in the foraging behaviour of different individuals. During observation sessions pangolin individuals did not appear to differ substantially in behaviour during my study, however, future studies should attempt to collect data from more individuals and across multiple years. Collection of data across multiple years may reveal different trends, as long-term and interannual factors may influence pangolin behaviour or prey abundance, especially in highly variable climates such as in the Kalahari (Panaino et al., 2022). Data for my study were collected after multiple years of above-average rainfall, which may have influenced pangolin foraging behaviour either directly or indirectly by affecting prey abundance. Future research should also investigate the amount of time pangolins spend at individual foraging sites, which will allow for an interpretation of the level of investment at each site and the productivity of individual sites. For instance, if a long time is spent at an individual site, one might predict that the site may have a greater concentration of prey, which may reduce a pangolin's need to forage over a greater distance. These additional data may provide a better understanding as to why there are seasonal variations in foraging behaviours. Similarly, determining the energetic costs of aspects of pangolin foraging behaviour, such as digging or foraging locomotion, may help explain trends in foraging behaviour.

Although there was no link between foraging frequency and prey abundance it is possible that prey abundance at its extremes, increased abundance (summer) and decreased abundance (winter), may both cause an increase in pangolin foraging frequency. This threshold response to prey abundance extremes may explain the two peaks in foraging frequency during summer and winter, as compared to the lower foraging frequency during autumn and spring, when prey was at intermediate levels. It is likely that the elevated prey abundance in summer leads to an increase in foraging frequency due to an increase in foraging opportunities for pangolins. In contrast, the increase in foraging frequency during winter, when prey abundance was at its lowest, might suggest that pangolins were required to increase how often they forage to compensate for the loss of easy foraging opportunities. Conversely, during periods of intermediate prey abundance, autumn and spring, the impact of prey abundance on foraging frequency may have been less pronounced. For pangolin foraging distance, it was likely that during seasons of increased prey abundance, pangolins travelled further due to ample foraging opportunities. As compared to when prey was scarce, the distance they travelled was reduced, as they may have shown increased investment in individual foraging sites when they came across an opportunity (foraged longer and travelled less). The observed increase in foraging distance during periods of increased prey abundance was contrary to the initial hypothesis. Instead of increasing foraging distance when prey is scarce, pangolins may rather change the duration and timing of their foraging activities in response to changes in prey abundance (Panaino, 2022). Pangolins are predominantly nocturnal but may become diurnal during the colder winter months (Pietersen et al., 2014b). Seasonal variation in pangolin 24h activity (Supplementary Table 1) is related to prey abundance, environmental temperatures and pangolin 24h minimum body temperature (Panaino, 2021). Additionally, pangolins have been observed to lower their 24h minimum body temperature during periods of food scarcity, possibly as a strategy to reduce energetic requirements by reducing metabolism and heat loss to the environment (Panaino et al., 2023). Hence, it is possible that instead of, or in addition to, changing their foraging frequency and foraging distance, pangolins may change their overall foraging duration and regulate body temperature less precisely (increased heterothermy) in response to changes in prey abundance (Panaino, 2021; Panaino et al., 2023).

The findings regarding pangolin foraging behaviour support the idea of energy investment in foraging activities, where high-energy foraging strategies, such as increased foraging frequency and distance, may be employed in times of abundant prey as it can be afforded (Norberg, 1977). In contrast, high-energy foraging methods, such as increased foraging frequency, are likely employed in times of decreased prey abundance out of necessity to maintain a minimum energy intake (Norberg, 1977). However, the use of foraging frequency as a proxy for energy investment is limited, as it does not consider the duration spent at each foraging site. Pangolins may increase their investment at individual foraging sites, by spending a longer duration foraging and excavating a greater amount of soil at each site. For example, armadillos (*Dasypus novemcinctus*) spend 77 to 90 % of their above-ground time foraging (Ancona and Loughry, 2009). Studies on fossorial animals, such as a South American rodent (*Ctenomys talarum*), have found that metabolic rates during digging can reach up to three times the resting metabolic rate (Luna et al., 2002). For the Chinese pangolin, both its field metabolic rate and resting metabolic rate are lower than that of other eutherian mammals of similar size, and comparable to that of anteaters (*Myrmecophaga tridactyla*) and armadillos (*Chaetophractus nationi*; Yan et al., 2023). One study on the metabolic rates of Temminck's pangolin revealed that this species has slightly lower metabolic rates than do other pangolin species, likely due to a larger body mass as compared to Chinese pangolins (Boyles et al., 2020). By recording the duration of foraging events and applying allometric scaling equations based on related species, it may be possible to estimate the energetic cost of foraging in pangolins. Additionally, accelerometers could be used to estimate energy expenditure by capturing detailed movement patterns during foraging activities.

Studies on the foraging behaviour of other fossorial and semi-fossorial animals have found that there is large variation in their digging behaviours. For example, the foraging frequency of woylies (*Bettongia penicillata*; a mycophagous species) ranges from 4 to 11 foraging sites per hour (Garkaklis et al., 2004), only slightly lower than that of pangolins (13 sites per hour). Foraging densities of echidnas are approximately between 125 to 400 digs ha^{-1} in semiarid rangelands (Eldridge and Kwok, 2008), while woylies can have a foraging density of up to 2 550 digs ha^{-1} (5 000 to 16 000 year^{-1}) in dry sclerophyll forests (Garkaklis et al., 2004). These foraging densities are substantially higher than that observed for pangolins (33 foraging sites ha^{-1}), however, when compared to other bioturbator species in the Kalahari, pangolin foraging densities are more similar. For example, bat-eared foxes, another myrmecophagous species in the Kalahari, have a foraging density of 94 digs ha^{-1} (Dean and Milton, 1991a). The species with the greatest similarity in foraging density to pangolins is the Cape porcupine, with a foraging dig density of 19 to 52 digs ha^{-1} (de Villiers and van Aarde, 1994). No data are available on the foraging density of aardvarks, a species that is ecologically similar to pangolins, with a large area of their distributions overlapping (Pietersen and Robertson, 2023; Knöthig, 2005; Taylor and Skinner, 2004). Direct comparisons between the foraging densities of species may be challenging, due to the large variation in the body mass, prey preference, foraging strategies and behaviours of the different species.

The trend of higher prey abundance in summer and lower prey abundance in winter is similar to what has been found previously in the Kalahari region (Panaino et al., 2022; Weyer, 2018). The overall preference for *Crematogaster* ants as prey was observed to be consistent with the findings of Panaino et al. (2022). Similarly, the seasonal shift in preference for *Anoplolepis* ants during winter also aligned with previous research (Panaino et al., 2022). Panaino et al. (2022) speculates that the switch in prey genera during winter may be as a result of *Anoplolepis* ants becoming more concentrated underground, in ‘pockets’, as they become less active on the surface during winter. As a result, pangolins may prefer to forage for or have easier access to these ‘pockets’ of *Anoplolepis* ants. The foraging sites associated with *Crematogaster* ants are generally bark scratchings, as compared to digging for *Anoplolepis* ants. Therefore, the switch to foraging on *Anoplolepis* ants may lead to increased digging activity, potentially altering the ecological role of pangolins through changes to their digging behaviour. The positive relationship observed between prey abundance and monthly average air temperature also aligns with the findings of studies related to myrmecophagous species in the Kalahari (Panaino et al., 2022; Weyer, 2018). Warmer air temperatures in summer increase the activity of ants (Cros et al, 1997; Lindsey and Skinner, 2001; Jayatilaka et al., 2011). The study by Panaino et al. (2022) on pangolins and Weyer (2018) on aardvark in the Kalahari found no significant effect of rainfall on prey abundance. However, other studies have shown that increased rainfall leads to a decrease in ant activity for certain species (Abhinandini and Venkatesha, 2013; Nunes et al., 2011; Farji-Brener et al., 2018). The elevated prey abundance during summer, despite the increase in rainfall, is likely as a result of harvesting ant species having increased food resources from the increase in vegetation growth due to higher rainfall (Fischer et al., 2022). The foraging behaviour of many species is dictated by the abundance of their prey, hence understanding the trend in prey abundance is important (Caldow and Furness, 2000; Goundie et al., 2015). Ultimately, the ecological impact of pangolin foraging behaviour will depend on prey abundance and, therefore, indirectly on climatic variables.

In the Kalahari, climate change models predict continued increases in air temperatures and decreases in rainfall, which is also expected to become increasingly sporadic and unpredictable (Engelbrecht et al, 2015; Mphale et al, 2014; Pattinson et al., 2022). Changes in climatic variables impact the abundance and availability of insects (Lindsey and Skinner, 2001; Nunes et al., 2011; Fischer et al., 2022), either directly or through the reduction of primary productivity, which decreases food resources (Tokura et al., 2018; Meloni et al., 2020; Oliveira et al., 2011). Potential decreases in prey abundance are likely to increase food scarcity for pangolins, leading to shifts in their foraging behaviours (Panaino, 2021). However, if pangolins are unable to adjust their foraging behaviours to cope with resource scarcities, it could lead to increased mortality. Hence, understanding how pangolin foraging behaviour responds to climate change, through its impact on prey abundance, is important to pangolin conservation.

The results of my study provide support for seasonal variability in pangolin foraging behaviour, and its link to prey abundance. Understanding the foraging behaviours and patterns of pangolins offers valuable insight into the different ways pangolins may contribute to their environment, through the potential ecosystem services that they provide. Therefore, changes in pangolin foraging behaviour, driven by shifts in prey abundance in the face of climate change, may impact the ecological role that pangolins provide.

CHAPTER 4

Seasonal variability in the ecosystem services that pangolins provide

Abstract

The functionality of an ecosystem relies on the ecosystem services provided by animals. Bioturbator species play a crucial role in the environment through their foraging behaviours, which contribute to resource capturing, decomposition and nutrient cycling. My study aimed to evaluate the ecosystem services that Temminck's pangolins, a bioturbator species, may provide through their foraging activities, namely soil turnover, biodiversity accumulation and nutrient cycling. I tagged and tracked four pangolins with VHF telemetry to observe them during their foraging activities. During observation sessions I measured the soil turnover, accumulated organic matter and soil nutrient concentration of foraging digs. The mean soil turnover generated per dig site by pangolins was 1.6 ± 2.0 kg, peaking in winter and decreasing in summer. Seasonal variation in soil turnover had a strong inverse relationship with prey abundance, which decreased during winter and increased during summer and autumn. The mean accumulation of organic matter in dig sites was 5.6 ± 4.9 g per dig site, and did not differ significantly across sample month (1, 4, 7 and 10 months post foraging event). Nitrogen concentration in pangolin dig sites (0.03 ± 0.01 %) did not differ to that of the surrounding undisturbed soils (control sites; 0.03 ± 0.01 %), while the total carbon concentration was 10.4 % (relative difference) higher in digs sites (0.20 ± 0.07 %) as compared to control sites (0.19 ± 0.05 %). Nitrogen concentration in dig sites decreased until 6 months post pangolin foraging event, whereas total carbon concentrations increased up to 3 months post foraging event before declining by 9 months. The ecosystem services of Temminck's pangolins, quantified in my study, are comparable to those of Chinese pangolins, however they may provide additional services, such as burrow maintenance and altering plant community structure. Overall, my study has shown that pangolins alter their

environment through the ecosystem services that they provide, and that these ecosystem services are influenced by prey abundance and the availability of organic material. Therefore, the important ecosystem services that pangolins provide may be lost if pangolin populations continue to decline, primarily because of the illegal wildlife trade.

4.1 Introduction

The ability of an ecosystem to function is closely linked to its biodiversity, which is essential for biomass production, resource capturing, decomposition and nutrient cycling (Cardinale et al., 2012). The loss of biodiversity compromises ecological systems and can lead to a collapse of the ecosystem (Cardinale et al., 2012). In an attempt to manage a cascading loss of biodiversity, conservation practices have begun to prioritize the preservation of species for the ecosystem services that they provide, especially in ecosystems that are at high risk of being compromised (Egoh et al., 2007). These ecosystems that are at high risk, such as dryland ecosystems, where animals already endure physiological challenges due to high temperatures and low rainfall (Ward, 2016), are particularly vulnerable to the effects of climate change (Pietersen et al., 2019a; Challender et al., 2020; Engelbrecht et al., 2015). In these ecosystems, the loss of species and the ecosystem services that they provide may have a disproportionately greater impact on overall ecosystem functionality.

Fossorial and semi-fossorial mammals are a group of specialist animals that are thought to provide a host of ecosystem services. These animals are believed to play an important role as ecosystem engineers due to their burrowing and digging activities, both for shelter and for foraging (Kinlaw and Grasmueck, 2012). Digging activities may provide ecosystem services by altering soil turnover, nutrient cycling and increasing local biodiversity (Fleming et al., 2013). An increase in soil turnover, as a result of digging behaviour, can alter the physiochemical makeup of soils (James et al., 2009). Alterations in soil physiochemistry can lead to improved nutrient cycling in the environment, making nutrients more accessible to other species in the system (Whitford and Kay, 1999). Macro- and micro-organisms, such as fungi, invertebrates and seeds accumulate in dig sites. Together with elevated nutrient concentrations as a result of the decomposition of organic matter, they can promote seed germination and plant recruitment over time (Martin, 2003; Ceballos, 1999). As a result, dig sites may have higher levels of biodiversity compared to undisturbed areas (Ceballos, 1999). Digging activities also impact hydrological aspects of the environment, increasing water infiltration and soil moisture, while decreasing surface run-off, resulting in increased water availability to plants and animals (Bond, 1964). All of these ecosystem services can significantly improve the resilience of an ecosystem to environmental change and disturbance, especially in dryland ecosystems such as the Kalahari, where my study was conducted.

Temminck's pangolin is a fossorial animal that engages in digging activities. Temminck's pangolins are nocturnal mammals and specialist feeders, found in a variety of habitats across eastern and southern areas of sub-Saharan Africa, at low population densities (Challender et al., 2020; Pietersen et al., 2020). Studies on other pangolin species, such as Chinese pangolin, show that pangolins impact their ecosystem through their role in nutrient cycling, soil turnover, insect population control and the accumulation of biodiversity in dig sites (Challender et al., 2020; Sun et al., 2021). The ecology of the Temminck's pangolin is similar to that of the Chinese pangolin (Challender et al., 2020), suggesting that Temminck's pangolin may also play a crucial role in their ecosystem. The foraging activities of Temminck's pangolins fluctuate in response to prey abundance (Panaino, 2021; Panaino et al., 2022), suggesting that their functional role may also vary in response to prey abundance.

For example, during winter ant colonies contract and move deeper underground (Heller and Gordon, 2006; Włodarczyk, 2021), which may result in increased digging activities by pangolins as they attempt to access food. However, despite Temminck's pangolin being the most widely researched pangolin species, their ecological role has never been quantified. The impact that the loss of pangolins may have on ecosystems through the loss of the ecosystem services that they provide is unknown, making quantifying those ecosystem services an important area of research.

In this chapter, I aimed to assess the ecosystem services that pangolins provide through their foraging activities. I evaluated pangolin ecosystem services by quantifying seasonal soil turnover, biodiversity accumulation and nutrient cycling inside pangolin foraging digs during foraging activity. I hypothesised that soil turnover would vary seasonally in relation to prey abundance and was predicted to increase as prey abundance decreased. Additionally, I hypothesised that pangolin foraging digs would increase biodiversity accumulation, concentrating organic matter within their foraging area across a year. Lastly, I predicted that pangolin foraging behaviour will promote nutrient cycling, by increasing the nitrogen and total carbon concentration of the soil within pangolin dig sites over time as compared to surrounding undisturbed soils.

4.2 Methods

4.2.1 Field sampling

4.2.1.1 Soil turnover

Four pangolins were located and followed with VHF telemetry during their active phase to identify 50 foraging sites per season, across one year (200 in total; Table 5). Seasons were defined as summer (December to February), autumn (March to May), winter (June to August) and spring (September to November). Sites were selected once an individual was observed digging, with soil turnover measurements taken after an individual was finished feeding at a dig site and had moved far enough away (~20 m) as not to be disturbed by the sampling procedure. Since the sampling at each site took three to five minutes, the subsequent site was selected once another dig was observed following the completion of the previous site's sampling. The number of foraging dig sites used for soil turnover sampling (n = 200), as well as that for biodiversity accumulation (n = 80) and soil nutrient sampling (n = 120), were based on similar sampling efforts performed on other pangolin species and fossorial animals (Dundas et al., 2022; Kraai, 2021; Sun et al., 2021). The prey genera associated with each dig site was recorded by identifying insects left over during feeding, using a field guide (Slingsby, 2017) and reference collection (Dedeben Research Centre). Prey genera were identified to account for potential variations in soil turnover at dig sites associated with different prey genera.

Table 5. The number of soil turnover measurements taken for different pangolin individuals, across different seasons.

Pangolin individual	**Soil turnover measurements**				**Total**
	Summer	**Autumn**	**Winter**	**Spring**	
HPW04	-	-	17	31	48
MM01	-	-	16	19	35
WG01	-	-	17	-	17
RS01	50	50	-	-	100
Total	50	50	50	50	200

To determine the soil volume turned over during digging activity, pangolin foraging digs were lined with a plastic bag (Kitchen bin bags, 660 mm x 810 mm, Tuffy, Nyanga, Cape Town) and filled with surrounding soil using a volumetric cylinder (plastic measuring cylinder, 1000 ml, Vitraform Glassware (PTY) Ltd, Johannesburg, South Africa; Figure 16).

To determine the average soil density across the vicinity where soil turnover measurements were taken, ten core soil samples were collected per season, across one year (40 in total), using a soil corer (t-shaped soil corer, homemade; Figure 17). Soil cores were taken at a depth of 20 cm, as I observed that pangolin digs sites were approximately 20 cm in depth, which corresponds to the average depth of *Anoplolepis* ant nests (Hoffmann, 2015). The length of each soil core, measured from the soil surface to the deepest point of the soil core along the vertical axis, was recorded. Given the diameter of the soil corer (18.83 mm), the soil core volume was calculated (volume = π x radius^2 x length). Soil core samples were weighed (Highland Portable Precision Balance, 0.001g precision, Adam Equipment, Milton Keynes, United Kingdom) and then dried in an oven (42 l compact oven, Swan Products Ltd, Staffordshire, United Kingdom) at 50°C for 40 h, until no further decrease in mass was observed due to evaporation of moisture. Once dried, the soil density was calculated using the dry mass and standardised core volume (density = mass/volume). The seasonal soil densities were then used to determine the mass of soil displaced at each dig during a given season (mass of displaced soil = seasonal soil density x volume of displaced soil). These methods have been successfully used to measure excavated soil densities of echidna in Australia (Dundas et al., 2022).

Figure 16. Soil turnover measurements taken using a volumetric cylinder. Photo credit Dawid Rossouw.

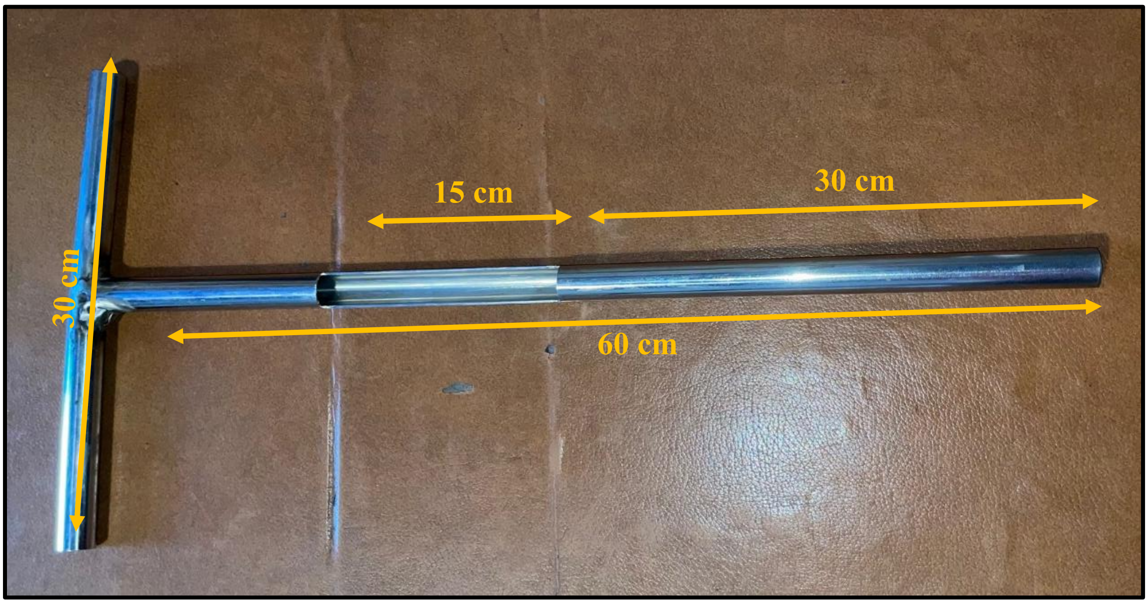

Figure 17. T-shaped soil corer, homemade. Photo credit Daniel Rossouw.

4.2.1.2 Biodiversity accumulation

Twenty dig sites were selected to quantify biodiversity accumulation, belonging to three pangolin individuals, with seven, seven and six sites per individual (Table 6). The selection of a site began 30 minutes after a pangolin was located or had exited its burrow, allowing time for the individual to become accustomed to my presence and begin creating foraging digs. Each selected site was at least 20 m from previously selected sites. In order to return to the selected dig sites for repeated sampling across time, the location of each site was taken, as well as marked with a physical marker (metal stakes, 150 cm in length and 1 cm in diameter, with an orange tag; Figure 18). The stakes were hammered into the soil such that only 50 cm were visible above the surface, to ensure that the markers could withstand trampling, while not hindering or injuring any animals passing by (Figure 18). One month after the dig had been created by a pangolin, all macro-organisms (such as insects, grass seeds, dung), accumulating inside the dig site were removed, weighed (SF-420 Electronic Compact Scale, 0.1g precision, Jiangyin Suofei Electronic Technology Co., Ltd, Jiangyin, Jiangsu, China) and recorded while in the field. After weighing all macro-organisms, all the removed material was put back inside the dig hole. Each dig site was returned to every three months (4, 7 and 10 months post foraging event), and repeat biodiversity accumulation measures were taken to assess any changes over time (Table 6). To observe any changes in dig size over time, the width (measured at the widest point perpendicular to the dig direction) and depth (measured from the deepest part of the dig hole to the level of the surrounding surface prior to excavation) of each dig site was measured (Figure 19a), and the dig condition (completely filled, mostly filled, partially filled, re-dug or dig lost) recorded. Dig sites were labelled as 'lost' if they could not be located for repeat sampling, due to physical markers being removed by animals. The direction of the dig was classified based on the position of the pangolin. The 'front' was defined as the point of the pangolin's head, the 'back' was defined as the direction in which the excavated soil is shovelled, and the 'left' and 'right' were defined relative to sides of the pangolin's body (Figure 19b).

Table 6. The number of biodiversity accumulation measurements taken for different pangolin individuals, at 1-month, 4-month, 7-month and 10-month post foraging event.

Pangolin individual	**Biodiversity accumulation measurements**				**Total**
	1-month (winter)	**4-month (spring)**	**7-month (summer)**	**10-month (autumn)**	
HPW04	7	7	7	7	28
MM01	6	7	7	7	27
WG01	6	6	6	6	24
Total	19	20	20	20	79

Figure 18. Biodiversity accumulation sampling site marked with a stake and orange tag. Photo credit Daniel Rossouw.

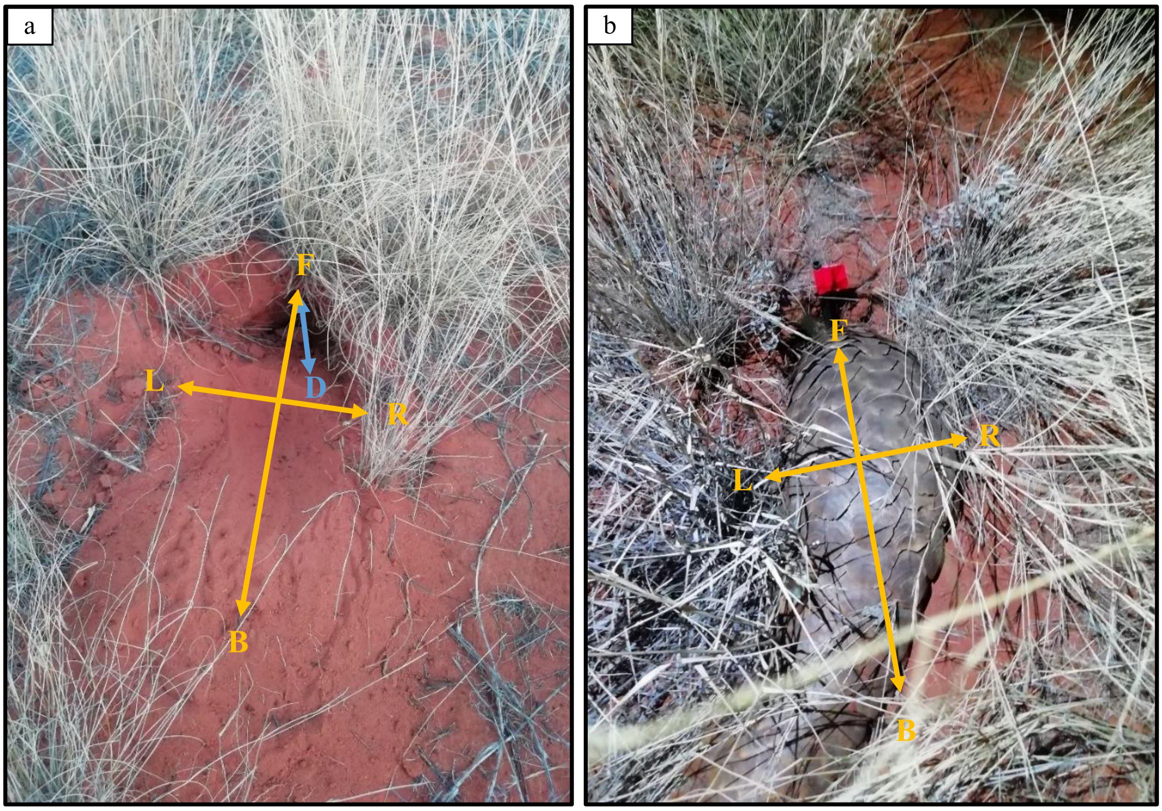

Figure 19. Orientation of a pangolin dig site (a), front (F), back (B), left (L), right (R) and depth (D), in relation to the body of a pangolin (b). Photo credits Daniel Rossouw.

4.2.1.3 Nutrient cycling

Fifteen dig sites were selected to measure soil nutrients (nitrogen and total carbon), from three pangolin individuals, with five sites per individual (Table 7). The selection of a site began 30 minutes after a pangolin was located or had exited its burrow, with each site at least 20 m away from previously selected sites, as described above. In order to return to the selected dig sites for repeated sampling across time, the location of each site was taken, in addition to marking the site with physical markers, as described above (Figure 18). At each of the 15 dig sites, a garden trowel (garden trowel RGT-004, Ryobi Africa (Pty) Ltd, Midrand, Johannesburg, South Africa) was used to take three soil samples (~100 g each, approximately half a trowel scoop), as well as three samples from the surrounding undisturbed soil, 2 m away (control site; Table 7; Figure 20). The same 15 sites were returned to every three months (0, 3, 6 and 9 months post foraging event), and repeat samples were taken to assess the change in nutrient content over time. A total of 120 soil nutrient measurements (30 per season) were taken, 60 from pangolin dig sites (three individuals) and 60 from surrounding undisturbed soils (control sites; Table 7). Soil samples were frozen at -24 ºC once collected (eco CF185HC chest freezer, Defy appliances (Pty) Ltd, Durban, South Africa) and stored until they could be transported to the laboratory for analysis at a later date. Soil analyses were conducted at the University of Stellenbosch, South Africa. Soil samples were defrosted and then dried at 50°C for 40 h (42 l compact oven, Swan Products Ltd, Staffordshire, United Kingdom). Any large organic matter and stones were removed, after which the samples were milled to a fine powder using a mortar and pestle (Figure 21). Approximately 60 mg of the homogenous milled soil sample was weighed (AP250D Analytical Plus balance, 0.0001g precision, Ohaus, Zurich, Switzerland) into an aluminium foil boat, along with 5 mg of an oxidation reagent and catalyst, Tungsten (VI)-oxide (WO_3) (Elemental Microanalysis Ltd., Okehampton, United Kingdom). An elemental analyser (Vario EL Cube CHNS Elemental analysis, Elementar, Frankfurt, Germany) combusted the sample, converting it into gaseous products. The reduced gases were separated using absorption columns and then detected by a thermal conductivity detector to determine the nitrogen ([N]) and total carbon (organic + inorganic carbon; [total C]) concentration (% of total sample). After every 15 samples, a duplicate sample, a blank (only Tungsten [VI]-oxide) and a standardised soil sample (2.02 % C, 0.183 % N, 0.41 % H and 0.029 % S) were used to calibrate the instrument and demonstrate method accuracy.

Table 7. The number of soil nutrient samples taken for different pangolin individuals, at time 0, 3-month, 6-month and 9-month post foraging event.

Pangolin individual	Soil nutrient samples (total = alternate + control sample)				Total
	Initial (winter)	3-month (spring)	6-month (summer)	9-month (autumn)	
HPW04	12 (6 + 6)	10 (5 + 5)	10 (5 + 5)	8 (4 + 4)	40 (20 + 20)
MM01	10 (5 + 5)	10 (5 + 5)	10 (5 + 5)	10 (5 + 5)	40 (20 + 20)
WG01	10 (5 + 5)	10 (5 + 5)	10 (5 + 5)	10 (5 + 5)	40 (20 + 20)
Total	32 (16 + 16)	30 (15 + 15)	30 (15 + 15)	28 (15 + 15)	120 (60 + 60) *

*Note that each sample had three replicates, totalling 360 samples.

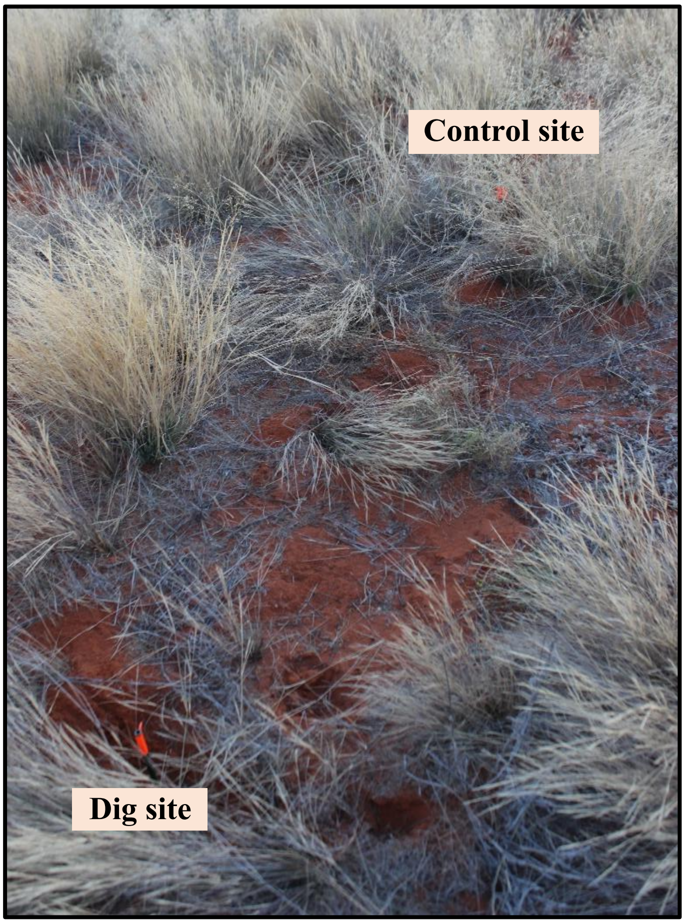

Figure 20. Soil nutrient sampling sites marked with stakes and orange tags, including both a pangolin dig site and a control site 2 m away. Photo credit Daniel Rossouw.

Figure 21. Soil nutrient sample milled to a fine power in a mortar and pestle. Photo credit Daniel Rossouw.

4.2.1.4 Prey abundance

Prey abundance was recorded to assess whether seasonal variations in soil turnover were linked to changes in prey abundance. Prey abundance was recorded monthly over an 11-month period using pitfall traps. For details on how prey abundance was recorded, refer to the methodology section in chapter 3.

4.2.2 Data analyses

All statistical analyses were performed using R (R Core Team, 2024), through the RStudio interface (v2023.6.1.524). A significance level of 0.05 was used throughout the statistical analyses.

4.2.2.1 Soil turnover

A linear mixed effect model was run to assess seasonal changes in soil turnover, using pangolin individual as a random effect, and its assumptions checked (lme4 package; Bates et al, 2015). The model assumption of normality was violated, and despite various transformations, could not be corrected for. Therefore, a non-parametric test, the Kruskal-Wallis rank sum test, was run to assess seasonal changes in soil turnover (base R; Supplementary Table 12). Post-hoc Dunn's tests of multiple comparisons were performed to identify significant differences between seasons (FSA package; Ogle et al., 2023). Additionally, the non-parametric Spearman's rank correlation test was used to investigate whether soil turnover was correlated to prey abundance (ants per trap seasonal average; base R; Supplementary Table 12). Seasonal ants per trap were used as the measure for prey abundance because it aligned with the soil turnover data, which were also spread across seasons.

4.2.2.2 Biodiversity accumulation

Linear mixed effect models were used to assess how the accumulated organic matter inside dig sites and dig size (width and depth) changed over time (lme4 package; Bates et al, 2015). Models were run with the accumulated organic matter, dig width and dig depth as the response variables, sample month (1, 4, 7 and 10 months post foraging event) as fixed effects, and pangolin individual as a random effect (Supplementary Table 12). Including pangolin individual as a random effect accounted for variability due to individual differences. The assumptions of linear mixed effects models were then checked. All three models (organic matter, dig width and dig depth) violated the model assumption of normality. The mass of organic matter was log transformed (log [accumulated organic matter per dig site + 1]) to correct for positively skewed data, with an added offset (+ 1) to ensure that all values remained non-zero and non-negative (Martin, 2021). Type II (marginal) analysis of variance (ANOVA) tests were used to assess any changes over time. Post-hoc Tukey's honestly significant difference tests were performed (emmeans package; Lenth, 2024) to identify where differences occurred between sample months. Despite applying various transformations for dig width and dig depth, normality could not be corrected for. Therefore, Kruskal-Wallis rank sum tests (non-parametric tests) were run to assess changes in dig width and dig depth over time (base R; Supplementary Table 12). Post-hoc Dunn's tests of multiple comparisons were performed to identify significant differences between sample months (FSA package; Ogle et al., 2023).

4.2.2.3 Nutrient cycling

Linear mixed effect models were used to compare the nitrogen and total carbon concentration (%) in dig sites as compared to the surrounding undisturbed soils (control sites), and how these percentages changed over time (lme4 package; Bates et al, 2015). Pangolin individual was included as a random effect to account for variability between individuals. However, due to insufficient variability in the random effect (boundary [singular] fit warming), it was removed, and linear models were used instead (base R). The decision to use linear models was supported by AIC values, which indicated that the linear models provided the best fit (Supplementary Table 13). The linear models were run with nitrogen and total carbon concentration as the response variables, sample type (dig site or control site) and sample month (0, 3, 6 and 9 months post foraging event) as fixed effects (Supplementary Table 12). When checking model assumptions, the models used to investigate carbon concentration violated the assumptions of normality and independent residuals. Therefore, a linear model using generalized least squares was run for the square-rooted carbon concentration (sqrt [carbon concentration + 0.03]), using AR(1) as the autocorrelation structure and sample month as the variance structure (nlme package; Pinheiro et al., 2023; Supplementary Table 12). The square-root transformation with an added offset (+ 0.03) was applied to correct for positively skewed data and to ensure that all values remained non-zero and non-negative (Martin, 2021). An added offset of 0.03 was used to avoid distorting the distribution, as the dataset contained several small values (<0.1). The relative difference (%) in nitrogen and total carbon concentrations between dig sites and control sites was calculated using the following formula: {([N or total C] of dig site – [N or total C] of control site) / [N or total C] of control site} x 100. Type II analysis of variance tests were used to compare dig and control sites and to assess any changes over time. Post-hoc Tukey's honestly significant difference tests were performed (emmeans package; Lenth, 2024), to identify where differences occurred over time.

A subset of the data (60 sites), consisting only of soil samples from pangolin digs sites, was taken to assess how the nitrogen and total carbon concentrations (%) in dig sites specifically changed over time. To analyse these changes, an additional linear model was fitted for nitrogen concentration, while a linear model using generalized least squares was used for the square-rooted total carbon concentrations (Supplementary Table 12). Both models utilised sample month (0, 3, 6 and 9 months post foraging event) as the predictor variable.

4.3 Results

4.3.1 Soil turnover

The 200 dig sites were within a total area of 45.8 km^2. The mean (± SD) soil turnover generated per dig site by pangolins was 1.6 ± 2.0 kg and varied seasonally (n = 200, Kruskal, df= 3, $X^2 = 70.08$, $p < 0.01$; Figure 22; Supplementary Table 14). Mean soil turnover generated per dig site was higher during winter (2.8 ± 2.3 kg per dig site) as compared to all other seasons (Figure 22; Supplementary Table 14; Supplementary Table 15). In contrast, the lowest mean soil turnover generated per dig site was during summer (0.7 ± 0.6 kg per dig site; Figure 22; Supplementary Table 14; Supplementary Table 15).

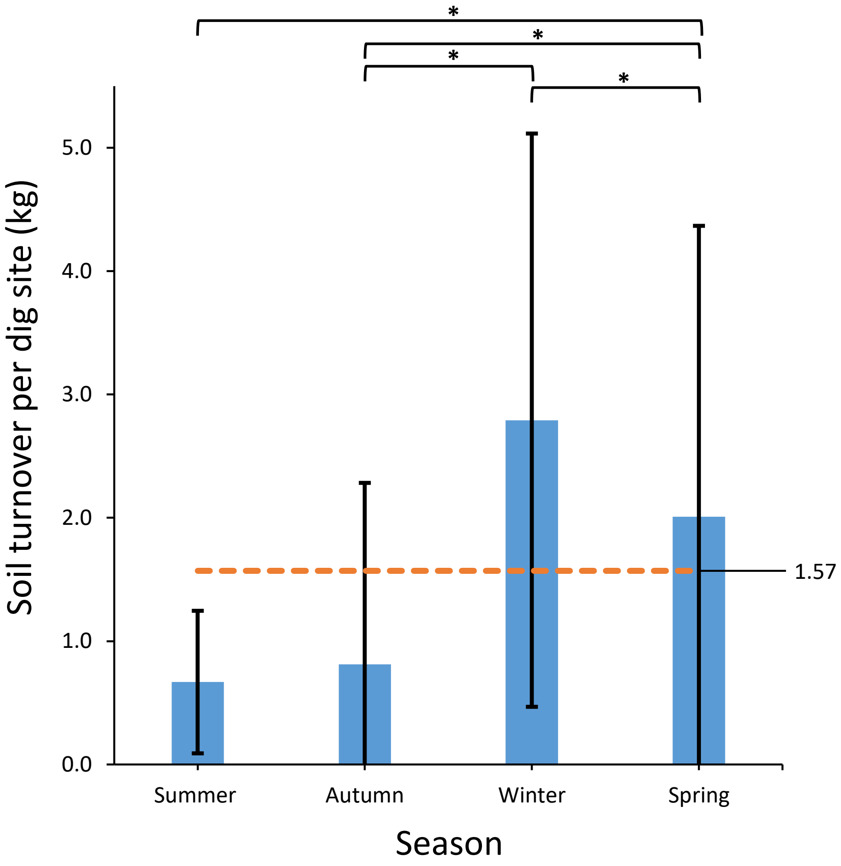

Figure 22. Mean soil turnover generated per dig site by pangolins across seasons. Error bars indicate standard deviation. The dashed orange line shows the mean soil turnover generated per dig site by pangolins across the year. Horizontal lines with asterisks indicate where soil turnover generated per dig site differed between seasons at a significance level of 0.05 (Bonferroni adjustment).

Of the 200 soil turnover measurements, 139 were associated with *Anoplolepis* ants, 26 with *Crematogaster* ants, 26 with *Trinervitermes* termites, and 9 with *Camponotus* ants. Of the four recorded pangolin prey genera, *Camponotus* ant foraging digs generated the largest soil turnover, followed by *Trinervitermes* termites, *Crematogaster* ants and *Anoplolepis* ants (Figure 23). Soil turnover had an inverse relationship with prey abundance (n = 200, Spearman, ρ = -0.44, S = 1 921 485.00, $p < 0.01$, $R^2 = 0.19$; Figure 24). Prey abundance increased during summer and autumn (28.7 ± 23.2 and 27.0 ± 28.1 ants per trap, respectively) and decreased during winter and spring (13.7 ± 17.3 and 13.4 ± 13.1 ants per trap, respectively), as discussed in chapter 3 (Supplementary Table 10).

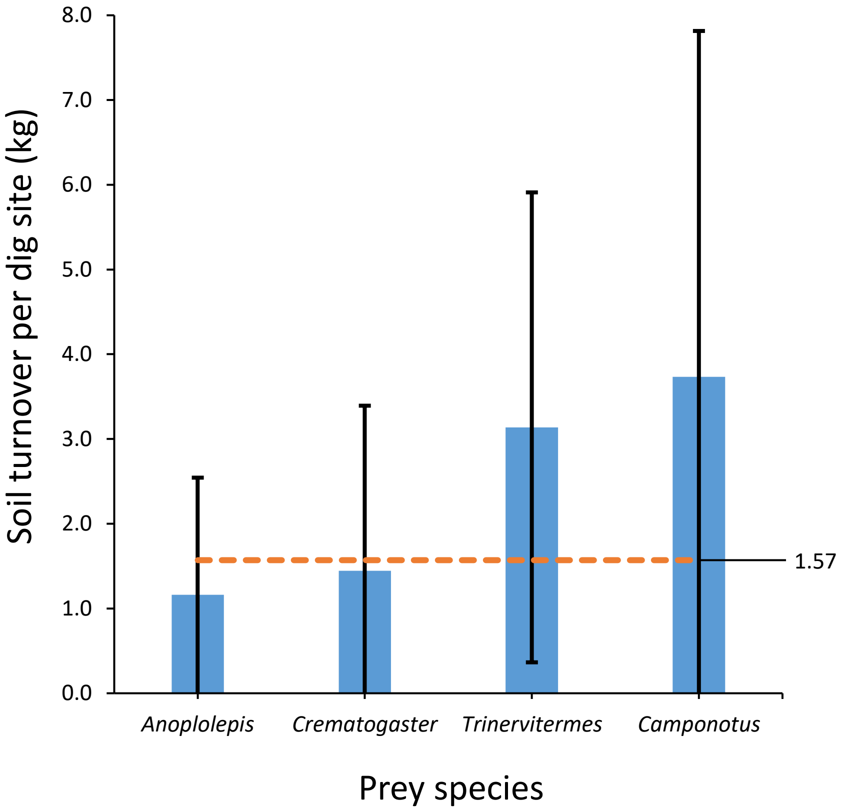

Figure 23. Mean soil turnover generated per dig site by pangolins for different prey genera. Error bars indicate standard deviation. The dashed orange line shows the mean soil turnover generated per dig site.

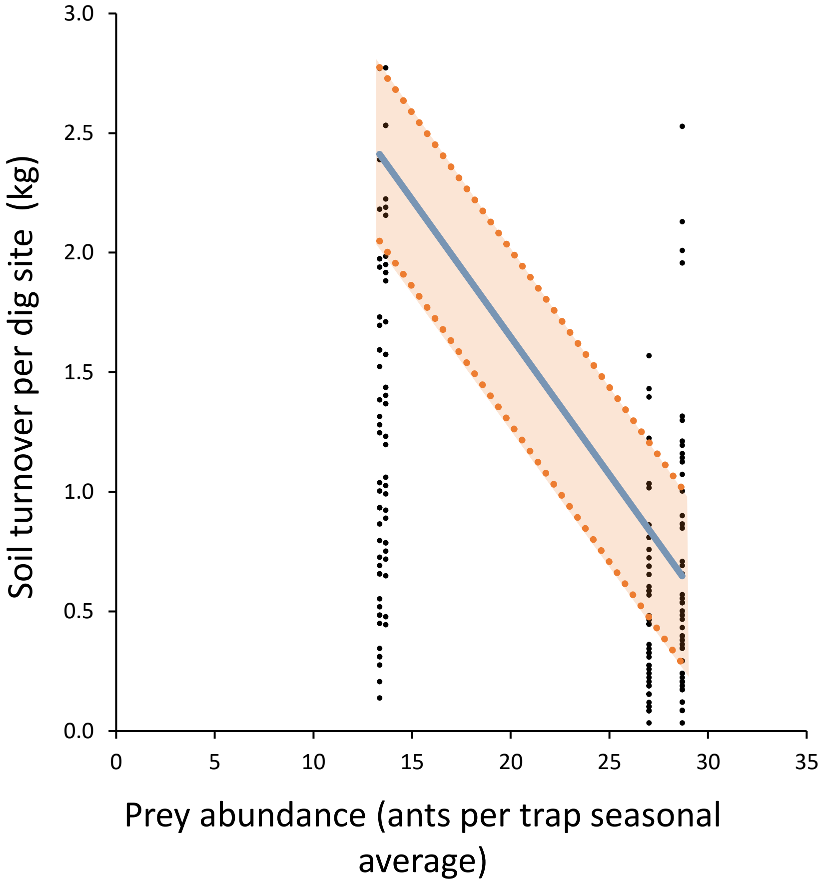

Figure 24. Linear relationship between the soil turnover generated per dig site by pangolins and prey abundance (ants per trap seasonal average). The dashed orange lines and shaded area show the 95% confidence interval.

4.4.2 Biodiversity accumulation

The 20 dig sites were within a total area of 27.7 km^2. The mean (± SD) biodiversity accumulation (accumulated organic matter) in pangolin dig sites was 5.6 ± 4.9 g per dig site, and showed no significant variation as time post pangolin foraging event changed (n = 79, Wald, df = 3, X^2 = 1.57, p = 0.67; Table 8; Figure 25; Supplementary Table 16). The mean dig width of pangolin dig sites (18.3 ± 6.6 cm) did not differ significantly as time post pangolin foraging event changed (n = 60, Kruskal, df= 3, X^2 = 6.40, p = 0.09; Figure 26; Supplementary Table 17; Supplementary Table 18), whereas the mean dig depth (6.0 ± 4.4 cm) did vary significantly as time post pangolin foraging event changed (n = 60, Kruskal, df=

3, $X^2 = 14.25$, $p < 0.01$; Figure 27; Supplementary Table 17; Supplementary Table 18). Dig depth was greatest at 1 month post foraging event (9.7 ± 3.1 cm), decreasing to its lowest at 7 months post foraging event (4.9 ± 5.1 cm; Figure 27; Supplementary Table 18). The count of dig sites that were completely filled, mostly filled, partially filled and re-dug all increased as time post pangolin foraging event increased (Figure 28).

Table 8. Descriptive statistics for the change in biodiversity accumulation (accumulated organic matter per dig site) of pangolin dig sites as time post foraging event (sample month) increased and averaged across the year.

Response variable	Sample month (months post foraging event)	Mean ± SD (g)	Median (g)	IQR (g)	Range (g)
Accumulated organic matter per dig site (g) (n = 79)	1	5.6 ± 5.2	3.3	2.4 to 6.6	0.6 to 19.3
	4	6.8 ± 5.8	5.2	2.7 to 9.2	0.9 to 21.2
	7	4.9 ± 4.1	4.5	2.1 to 6.6	0.0 to 14.9
	10	5.0 ± 4.1	4.1	2.9 to 6.2	0.0 to 16.6
	Average	5.6 ± 4.9	3.9	2.3 to 7.0	0.0 to 21.2

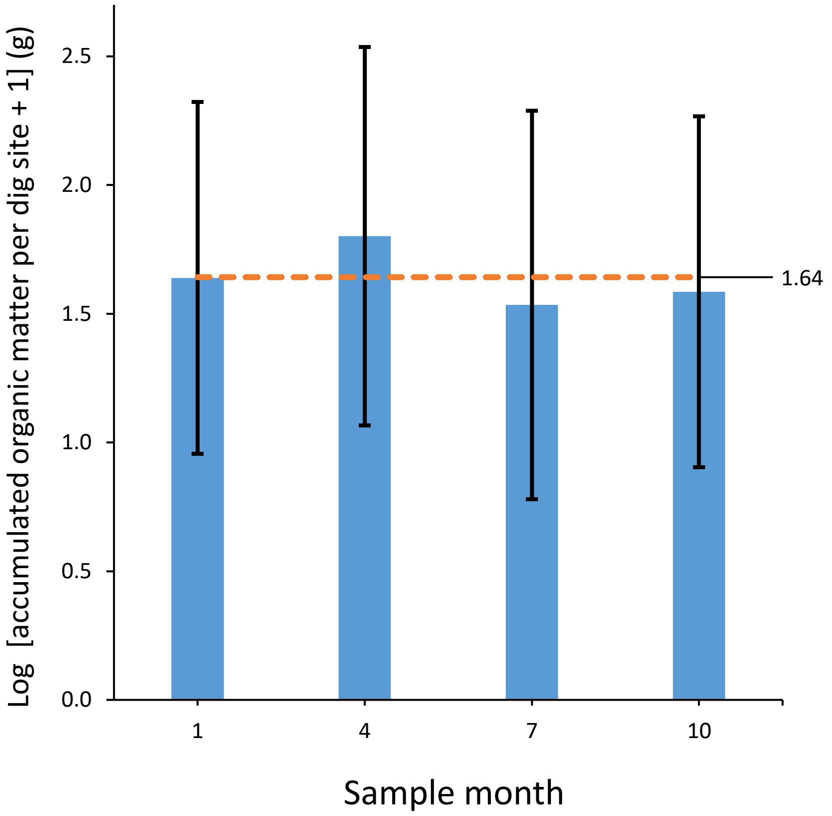

Figure 25. Mean logged accumulated organic matter (log [accumulated organic matter per dig site + 1]) in pangolin dig sites as time post foraging event (sample month) increased. Error bars indicate standard deviation. The dashed orange line shows the mean biodiversity accumulation (accumulated organic matter) per pangolin dig site across the year.

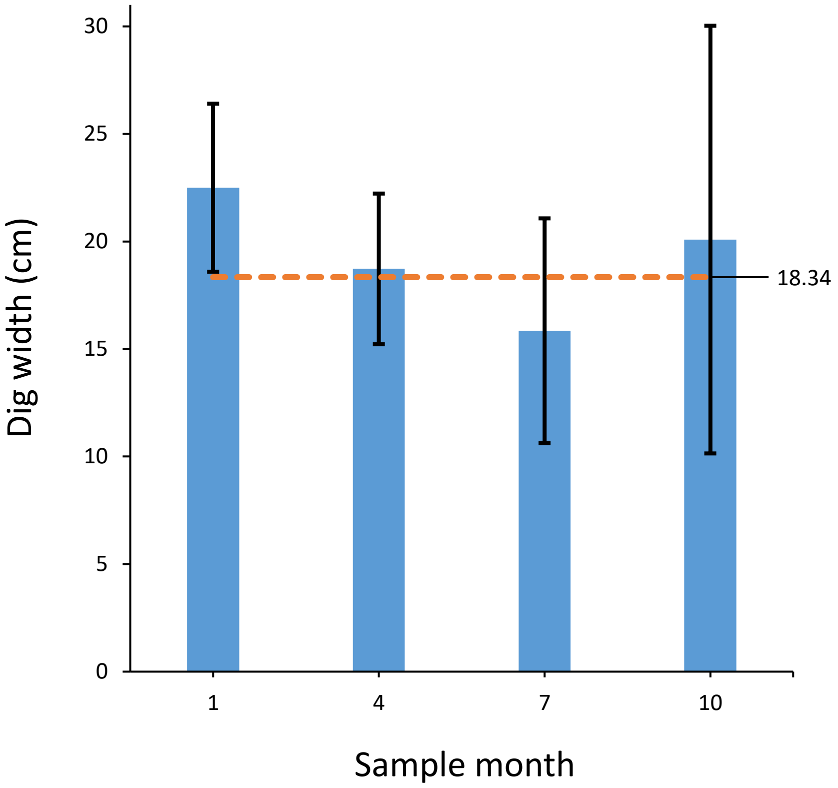

Figure 26. Mean dig width of pangolin dig sites as time post foraging event (sample month) increased. Error bars indicate standard deviation. The dashed orange line shows the mean dig width (cm) of pangolin dig sites across the year.

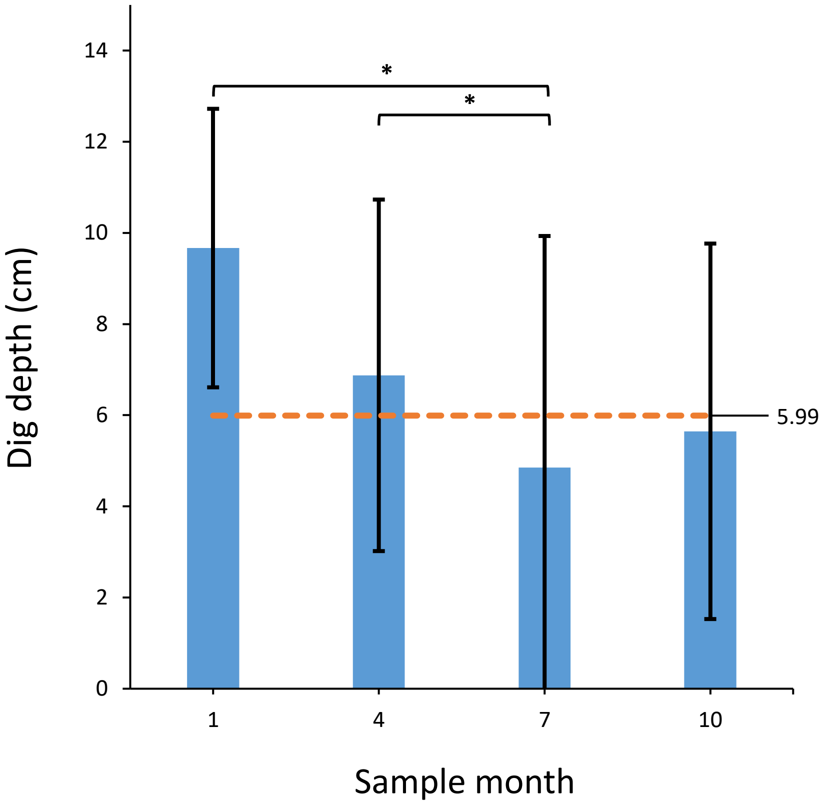

Figure 27. Mean dig depth of pangolin dig sites as time post foraging event (sample month) increased. Error bars indicate standard deviation. The dashed orange line shows the mean dig depth (cm) of pangolin dig sites across the year. Horizontal lines with asterisks indicate where pangolin dig width differed between sample months at a significance level of 0.05 (Bonferroni adjustment).

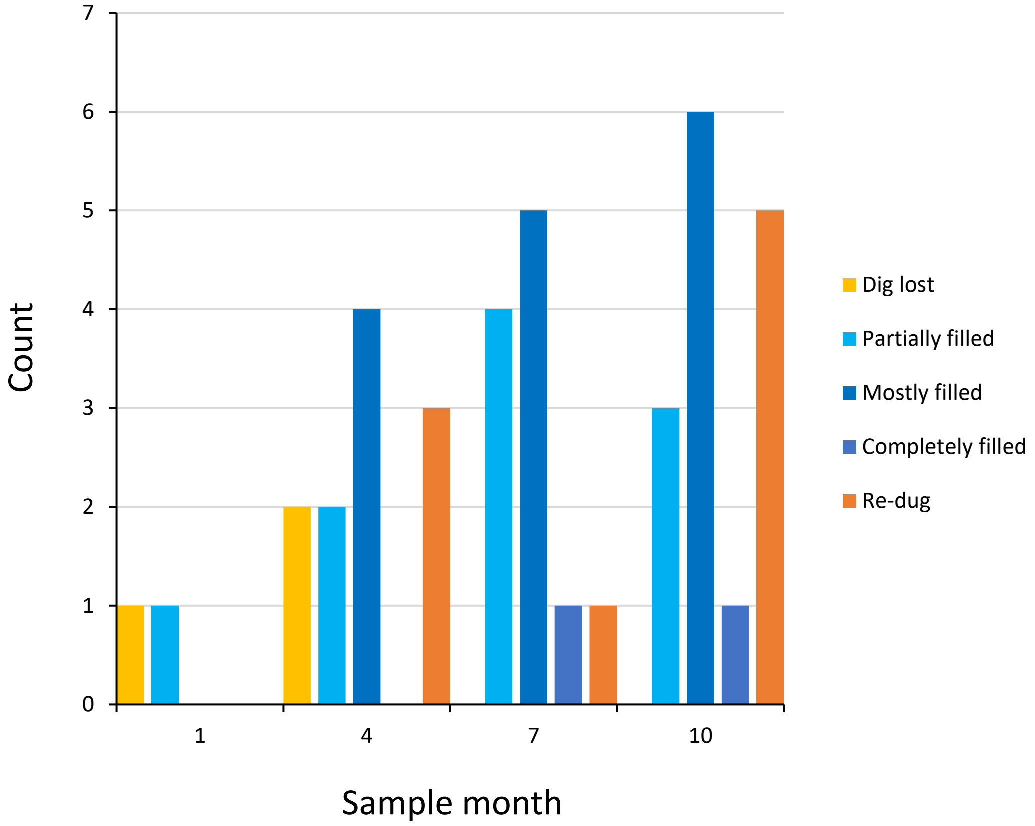

Figure 28. Count of pangolin dig sites of different dig conditions (completely filled, mostly filled, partially filled, re-dug or dig lost) as time post foraging event (sample month) increased.

4.3.3 Nutrient cycling

The 15 dig and control sites covered a total area of 28.4 km^2. The mean (± SD) nitrogen concentration in pangolin dig sites (0.03 ± 0.01 %) was not significantly different to that of the control sites (0.03 ± 0.01 %; $n = 120$, ANOVA, $df = 1$, $F = 0.04$, $p = 0.83$, $R^2 = 0.44$; Table 9; Supplementary Table 19). In contrast, the total carbon concentration differed significantly between dig sites (0.20 ± 0.07 %) and control sites (0.19 ± 0.05 %; $n = 120$, ANOVA, $df = 1$, $X^2 = 3.82$, $p = 0.05$, $R^2 = 0.44$; Table 9; Supplementary Table 19). However, both nitrogen and total carbon concentrations varied significantly as time post pangolin foraging event changed (ANOVA, $df = 3$, $F = 32.88$, $p < 0.01$, $R^2 = 0.44$ and ANOVA, $df = 3$, $X^2 = 85.19$, $p < 0.01$, $R^2 = 0.87$, respectively; Supplementary Table 19). The mean relative difference in total carbon concentration between dig sites and control sites was 10.4 % (with a higher concentration in dig sites; Table 9). The relative difference in total carbon concentration between dig sites and control sites was lowest at 0 months (initial measurement; 3.5 % higher in control sites) and greatest at 6 months post foraging event (17.6 % higher in dig sites; Table 9).

Table 9. Descriptive statistics of the nitrogen and total carbon concentration (untransformed) in pangolin dig sites in contrast to surrounding undisturbed soils (control sites) as time post foraging event (sample month) increased and averaged across the year.

Response variable	Sample month (months post foraging event)	Sample type (mean ± SD) (%)		Relative difference [(dig site – control site)/control site] (%)
		Dig site	**Control**	
Nitrogen concentration (%) (n = 120, 30 per sample month)	0	0.04 ± 0.01	0.04 ± 0.01	-5.6
	3	0.04 ± 0.01	0.04 ± 0.01	-1.2
	6	0.02 ± 0.01	0.02 ± 0.01	4.4
	9	0.03 ± 0.01	0.03 ± 0.01	2.8
	Average	0.03 ± 0.01	0.03 ± 0.01	-1.2
Total carbon concentration (%) (n = 120, 30 per sample month)	0	0.13 ± 0.06	0.14 ± 0.05	-3.5
	3	0.25 ± 0.05	0.22 ± 0.04	12.1
	6	0.24 ± 0.05	0.20 ± 0.04	17.6
	9	0.20 ± 0.07	0.18 ± 0.02	11.6
	Average	0.20 ± 0.07	0.19 ± 0.05	10.4

In the subset for pangolin dig sites only, both the nitrogen concentration and total carbon concentration (n = 60) varied significantly as time post pangolin foraging event changed (ANOVA, df = 3, F = 13.39, $p < 0.01$, $R^2 = 0.37$ and ANOVA, df = 3, $X^2 = 57.84$, $p < 0.01$, $R^2 = 0.87$, respectively; Figure 29; Figure 30; Supplementary Table 20; Supplementary Table 19). Nitrogen concentration was highest at 0 months (initial measurement; 0.04 ± 0.01 %), decreasing to its lowest at 6 months post foraging event (0.02 ± 0.01 %; Figure 29; Supplementary Table 20; Supplementary Table 21). The total carbon concentration was lowest at 0 months (initial measurement; 0.13 ± 0.06 %), increased to its highest at 3 months post foraging event (0.25 ± 0.05 %) and subsequently decreased towards 9 months post foraging event (0.20 ± 0.07 %; Figure 30; Supplementary Table 20; Supplementary Table 21).

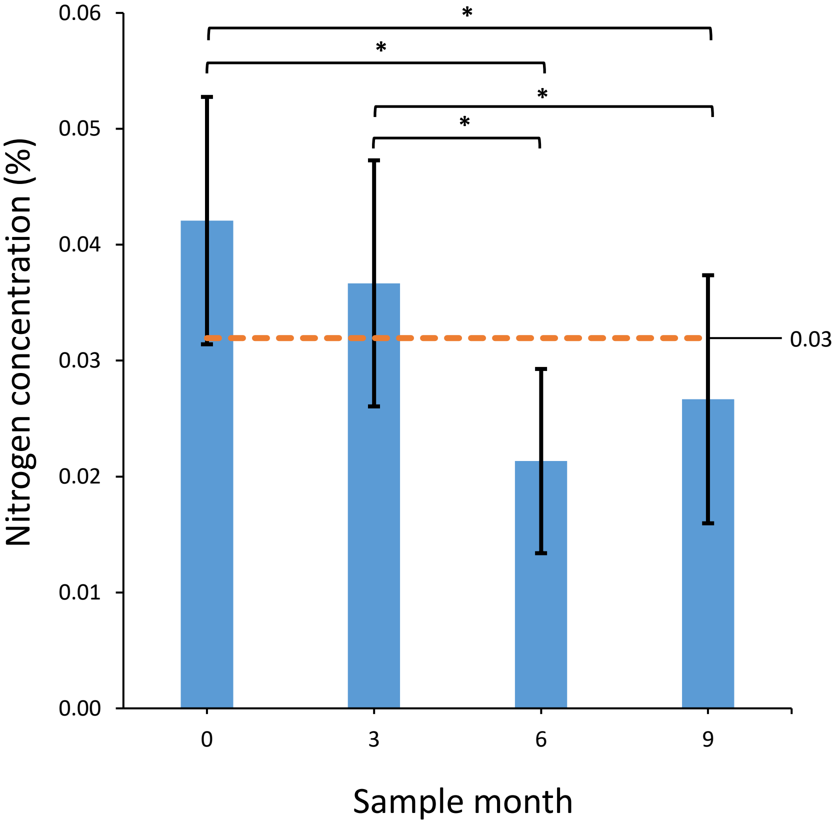

Figure 29. Mean nitrogen concentration in pangolin dig sites as time post foraging event (sample month) increased. Error bars indicate standard deviation. The dashed orange line shows the mean nitrogen concentration in pangolin dig sites across the year. Horizontal lines with asterisks indicate where nitrogen concentration in pangolin dig sites differed between sample months at a significance level of 0.05 (Tukey adjustment).

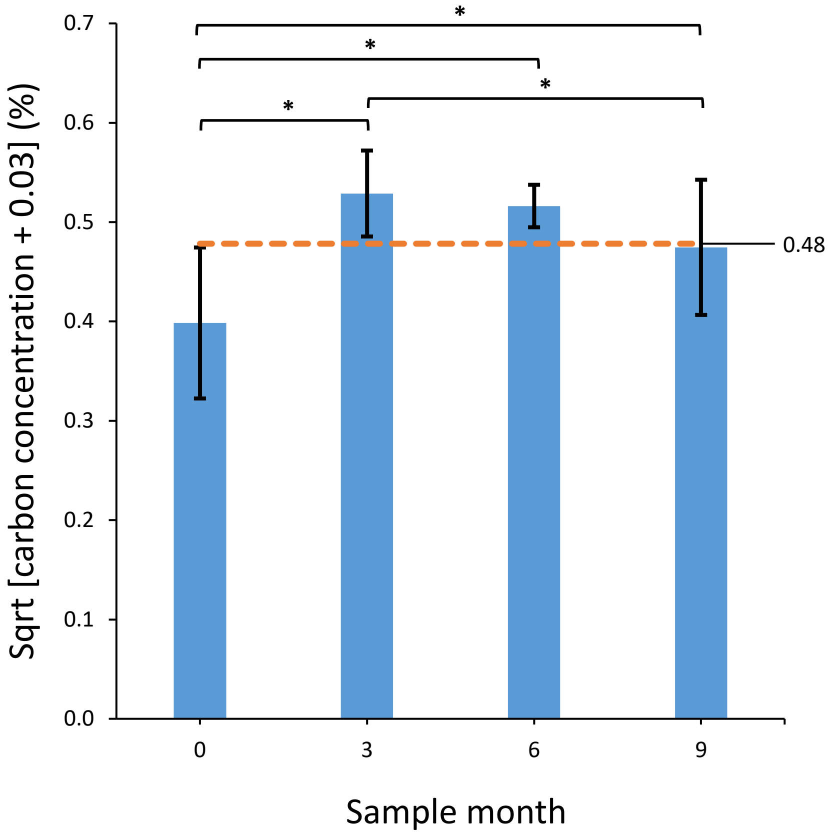

Figure 30. Mean square-rooted total carbon concentration (sqrt [carbon concentration + 0.03]) in pangolin dig sites as time post foraging event (sample month) increased. Error bars indicate standard deviation. The dashed orange line shows the mean square-rooted total carbon concentration in pangolin dig sites across the year. Horizontal lines with asterisks indicate where square-rooted total carbon concentration in pangolin dig sites differed between sample months at a significance level of 0.05 (Tukey adjustment).

4.4 Discussion

The soil turnover generated per pangolin dig site varied seasonally and was linked to prey abundance, lending support to the initial hypothesis. The amount of soil turnover generated by pangolins peaked during winter, coinciding with when prey abundance was at its lowest. Conversely, during periods where prey abundance was at its highest, summer and autumn, there was a decrease in soil turnover. The accumulated organic matter inside pangolin foraging digs did not vary significantly as time post foraging event increased, providing no support for the hypothesis that foraging digs promote biodiversity accumulation. However, this result can likely be explained by sites being re-dug, as a quarter of sites were re-dug within ten months. The highest accumulation of organic matter in pangolin dig sites occurred four months post foraging event, but had decreased by seven months post foraging event, likely as a result of dig holes becoming filled with sand. This idea is supported by the steady decrease in dig depth as time post foraging event increased, except for ten months post foraging event. Sites being re-dug likely contributed to the slight increase in accumulated organic matter observed from seven to ten months post foraging event, as newly dug holes provide additional space for organic matter to accumulate.

Nitrogen concentration of the soil in pangolin dig sites did not differ to that of the surrounding undisturbed soils. Nitrogen concentration in pangolin dig sites steadily decreased up until six months post foraging event, but so did the nitrogen concentration of the surrounding undisturbed soils. Therefore, the foraging digs of pangolins seem to have no impact on the cycling of nitrogen in the environment, contrary to the original hypothesis. The total carbon concentration was 10.4 % higher in the soil of pangolin dig sites as compared to the surrounding undisturbed soils, supporting the hypothesis that pangolin foraging behaviour increases soil carbon concentrations over time. Total carbon concentration in the soil of pangolin dig sites showed a significant increase from initial measurements to three months post foraging event, after which total carbon concentration steadily decreased over time. The change in total carbon concentration over time in control sites was similar to that for pangolin digs sites, however overall total carbon concentrations were lower.

Certain limitations should be considered when interpreting these findings. The greatest limitation of my study was the small sample of studied pangolins and the lack of consistent observations per pangolin individual across seasons. Data was not collected across all seasons for any of the pangolin individuals, with large portions of data for some individuals obtained during only one or two seasons. The small number of individuals in my study was as a consequence of difficulty in locating pangolins to tag, as well as study individuals being predated, dispersing, or inhabiting inaccessible areas of the reserve. This limits the interpretation of the seasonal effect as variation in the foraging behaviour of different individuals may be the cause. However, from my observations, pangolin individuals did not appear to vary substantially in their foraging behaviour. While it is acknowledged that finding and tagging pangolins is immensely difficult due to their solitary, nocturnal and scarce nature, future studies should attempt to collect data from more individuals and across multiple years. Another major limitation was the lack of data collection of biodiversity accumulation for the surrounding undug surface (control sites). This lack of control sites was an oversight during field sampling and prevents direct comparison of biodiversity accumulation in pangolin dig sites and the surrounding surface. Hence, conclusive support for the hypothesis that pangolin foraging digs will increase the biodiversity accumulated within the environment cannot be shown. Despite this oversight, the findings do provide evidence that pangolin foraging digs aid in accumulating and assimilating organic matter. Moreover, a large proportion of the accumulated organic matter in pangolin foraging digs was made up of grass seeds. While the number of seeds was not counted during my study, their accumulation could potentially affect plant community structure, highlighting the need for further investigation.

The seasonal variation in soil turnover likely reflects shifts in pangolin foraging behaviour in response to changes in prey abundance. Myrmecophagous species experience resource scarcity during winter as a result of a reduction in ant and termite activity and abundance (Lindsey and Skinner, 2001; Pietersen et al., 2016b; Weyer, 2018; Taylor et al., 2002). In winter, ant colonies contract and move deeper underground (Heller and Gordon, 2006; Włodarczyk, 2021; Panaino et al., 2022). This behaviour is a strategy for insects to shelter from extreme temperature fluctuations, particularly the temperature declines during winter, as deeper chambers maintain stable temperatures as compared to surface chambers (Włodarczyk, 2021). The contraction of ant colonies leads to an increase in localised ant densities (Heller and Gordon, 2006; Markin, 1970). Pangolins may be investing more energy and time at individual foraging sites during periods of decreased prey abundance, in an attempt to maximise gains when prey is located. As a result, pangolins dig deeper to access ant colonies, leading to elevated levels of soil turnover during winter.

The estimated yearly soil turnover generated by a single pangolin was 15 619 ± 10 788 kg (15.6 ± 10.8 metric tonnes; Supplementary Table 22). The yearly soil turnover generated by a single pangolin during foraging was estimated by multiplying the mean soil turnover generated per *Anoplolepis* ant foraging site by the estimated yearly number of *Anoplolepis* ant foraging sites (Supplementary Table 23). Foraging sites associated with *Anoplolepis* ants were used as they were exclusively associated with dig sites, whereas other prey genera were more commonly associated with bark scratching. Foraging soil turnover estimates for other fossorial species include woylies (~1.3 kg body mass), with an estimated turnover of 4.8 tonnes of soil individual^{-1} year^{-1} (Garkaklis et al., 2004), and southern brown bandicoot (*Isoodon obesulus*; ~1.4 kg body mass) with a soil turnover of 3.9 tonnes of soil individual^{-1} year^{-1} (Valentine et al., 2013). These estimates are lower than that for pangolins (~6 kg body mass), 15.6 tonnes of soil individual^{-1} year^{-1}. However, when the soil turnover is expressed relative to body mass, the soil turnover is more comparable (3.7, 2.8 and 2.6 tonnes of soil individual^{-1} kg body mass^{-1} year^{-1}, for woylies, southern brown bandicoot and pangolin, respectively). These values align with estimates for fossorial mammals in general, which range from 1.8 to 3.6 tonnes of soil per kg body mass per year while foraging (Fleming et al., 2013). Differences in the soil turnover generated by these species is likely explained by differences in their diet. Pangolins tend to dig shallow holes in search of ants and termites (<20 cm; Swart et al., 1999), whereas woylies and bandicoots forage for subterraneous fungi, plant material and invertebrates (Zosky et al., 2018; Mallick et al., 1998). Pangolins are estimated to turnover 0.02 tonnes ha^{-1} year^{-1}, which is considerably lower than the 1.23 tonnes of soil ha^{-1} year^{-1} for short-beaked echidnas (2 to 7 kg), another myrmecophagous species (Dundas et al., 2022). However, these differences may be as a result of echidnas having smaller home ranges (0.7 km^2) than pangolins (6.5 km^2), leading to a greater concentration of dig sites and soil turnover (Abensperg-Traun, 1991; Badgery et al., 2021; Eldridge and Kwok, 2008).

Studies of other fossorial animals have found that foraging digs can have substantially elevated amounts of organic matter as compared to the undisturbed surface (Fleming et al., 2013). A study on greater bilby (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) showed that organic litter was nearly exclusively found in dig sites (16.1 g), rather than on the surrounding surface (0.1 g; James and Eldridge, 2007). The foraging digs of these species supported over three times the number of seedlings (2.6 seedlings) as the surrounding surface (0.7 seedlings; James et al, 2010). The foraging digs of short-beaked echidnas accumulate twice the amount of organic matter (37.2 g) compared to the equivalent surrounding surface (18.0 g; Eldridge and Mensinga, 2007). The mean accumulated organic matter inside pangolin foraging digs (5.6 g), and when expressed relative to dig volume (<0.01 g cm^{-3}) was less than for greater bilby and burrowing bettongs (0.05 g cm^{-3}; Newell, 2008; James and Eldridge, 2007). However, direct comparison of the accumulated organic matter should be approached cautiously due to differences in field sampling methods, as well as variations in the plant species present in different habitats. Additionally, the accumulation of organic matter in digs sites of various ages is likely to be dependent on the seasonal life cycles of the vegetation. For example, a new dig site may accumulate less organic matter as compared to an older partially filled one, due to the timing of when grasses disperse their seeds. Hence, future research on how plant phenology affects the accumulation of biodiversity in pangolin dig sites should be conducted. Such research may lead to an understanding of during which seasons, or stages of plant phenology, pangolin foraging digs may be elevating the accumulation of biodiversity in the environment.

One possible explanation for the changes in total carbon concentration in pangolin dig sites over time is the build-up of nutrients in dig sites as a result of the accumulation of organic matter. The accumulated organic matter in dig sites likely became buried as dig sites were filled by sand over time. The burial of organic matter exposes it to soil microbes and invertebrates, enhancing its decomposition (Eldridge and Mensinga, 2007). As organic matter decomposes it leads to the formation of humus, elevating soil organic matter, which in turn increases the total carbon concentration of the soils (Nielsen et al., 2011; de Haan, 1977; Haynes, 1986). In contrast, the nitrogen cycle in arid environments follows a different pattern. As organic matter decomposes, increased temperatures increase the loss of nitrogen to the atmosphere through volatilization (West, 1991). Therefore, it is likely that the nitrogen cycling in soil is more closely linked to nitrogen fixation by plants or atmospheric deposition via rainfall (Schlesinger et al., 2006; West, 1991), rather than the foraging behaviour of pangolins.

The digging activities of bioturbator species, under certain conditions, can result in either elevated or reduced nutrient levels in disturbed soils as compared to undisturbed soils. For example, bioturbation by Plateau pikas (*Ochotona curzoniae*) and badgers (*Taxidea taxus*) creates patches of bare soil, leading to a decreased soil carbon and nitrogen concentration (Yu et al., 2017; Eldridge and Whitford, 2009). The decrease in soil nutrients is likely as a result of digging actions displacing the topsoil with deeper, nutrient-deficient soils or through the direct removal of organic material (Yu et al., 2017; Eldridge and Whitford, 2009). The nitrogen concentration in woylie dig sites decreased as compared to the surrounding soils, due to increased water infiltration leading to leaching of nutrients from the soils (Garkaklis et al., 2003). The digging activities of northern pocket gophers (*Thomomys talpoides*) increased the total carbon and nitrogen concentrations of soils by 13 % and 11 %, respectively, compared to undisturbed soils, primarily through the burial of plant material (Yurkewycz et al., 2014). The 13 % increase in carbon concentration in gopher digs is similar to that found for pangolin digs (10.4 %), yet pangolin digs showed no increase in nitrogen concentration while gopher digs did. Rodents in desert ecosystems have also been shown to increase the decomposition rate and turnover of organic matter (Steinberger and Whitford, 1983). In the Cape Fynbos biome, South Africa, the nitrogen concentration in the mounds of common mole rats and Cape mole rats was higher than that of undisturbed soils, and their presence enhanced plant species richness (Hagenah and Bennett, 2012).

Overall, my study has shown that pangolins, like other fossorial and myrmecophagous species, contribute to their environment through the ecosystem services that they provide, namely soil turnover, nutrient cycling and potentially biodiversity accumulation. The ecosystem services that they provide appear to be linked to prey abundance, which is linked to climatic variables (Panaino et al., 2022; Weyer, 2018; Nunes et al., 2011). Therefore, as the threat of biodiversity loss and climate change continues, it is increasingly likely that vital ecosystem services will be lost as well.

CHAPTER 5

Conclusion

As the threats to global biodiversity continue, the resulting loss of species along with their ecosystem services will disrupt overall ecosystem stability. Conservation strategies prioritizing species that provide crucial ecosystem services act as a strong defence against such threats, as the protection of a single species can provide protection for many other species and processes in the ecosystem. Rare species are often assumed to have minimal impact on ecosystem functionality due to their low densities in the environment. However, rare species are frequently among those most in need of conservation efforts. The assumption that rare species provide a limited contribution to the ecosystem raises questions about their prioritisation in conservation efforts. One such species is the Vulnerable Temminck's pangolin, which is protected under CITES appendix 1. My study provides the first empirical evidence of the ecological role that Temminck's pangolins play in a dryland ecosystem. The results of my study provide support for continued and elevated conservation efforts for Temminck's pangolins.

One of the key areas for pangolin conservation that requires attention, as identified by the IUCN Pangolin Specialist Group, is that of ecological research. An improved understanding of pangolin behaviour, the species' ecological role and threats in the environment can contribute to better conservation strategies (Shirley and Parker, 2024). My study contributes to filling that gap, as it has shown that pangolins play an important role in the dryland Kalahari ecosystem by providing crucial ecosystem services, through soil turnover, biodiversity accumulation and nutrient cycling. I estimated that a single pangolin uses 29 855 ± 8281 foraging sites each year (Supplementary Table 23), turning over 15.6 ± 10.8 metric tonnes of soil (15 619 + 10 788 kg; Supplementary Table 22), and that their foraging digs accumulate 66.1 ± 62.8 kg of organic matter each year (Supplementary Table 24; estimated using the results from my study for one year). The estimate of soil turnover generated by pangolins is likely an underestimation, as soil turnover was only calculated for foraging sites associated with *Anoplolepis* ants and not for sites associated with other prey genera. Foraging sites associated with *Anoplolepis* ants were selected as they were exclusively associated with dig sites, whereas other prey genera were more frequently, but not exclusively, associated with bark scratching. The soil turnover generated by pangolins per kg body mass across a year (2.6 tonnes of soil individual^{-1} kg body mass^{-1} year^{-1}) aligns with the general estimates for fossorial mammals, of 1.8 to 3.6 tonnes of soil per kg body mass per year while foraging (Fleming et al., 2013). Aspects of pangolin foraging behaviour coincided with changes in prey abundance, such as increased soil turnover and decreased foraging distance during winter when prey abundance declined. It is predicted that dryland environments, such as the Kalahari, will continue to experience rising air temperatures, increased evapotranspiration, and greater variability in rainfall events, such that resource abundance will be impacted (Engelbrecht et al., 2015; Mphale et al., 2014; Cahill et al., 2013). Shifts in prey abundance, driven by changes associated with climate change, may cause changes in pangolin foraging behaviour, which in turn may affect the ecological role that pangolins play.

Future research should investigate how seasonal activity and abundance of pangolin prey genera may shift due to climatic changes. For instance, as air temperatures rise, the above-ground activity of ant and termite genera may change (Lindsey and Skinner, 2001; Swart et al., 1999). The normally low winter activity of *Crematogaster* ants (an arboreal ant genus) may increase as temperatures rise in winter. *Crematogaster* ants have a high critical thermal maximum (51.2 °C; Roeder et al., 2021), while *Anoplolepis* ants have lower critical thermal maximum (a terrestrial ant genus; 48.3 °C; de Bie and Hewitt, 1990). As a result, there may be a shift in the dominant prey genera of pangolins, causing *Crematogaster* ants to become the dominant prey species across all seasons, instead of the current shift to *Anoplolepis* ants in winter (Panaino et al., 2022). If pangolins forage more on *Crematogaster* ants there is likely to be a reduction in soil turnover generated by pangolins, due to a reduction in the digging activities associated with *Anoplolepis* ants. However, the opposite impact may also be observed, as *Anoplolepis* ants might tolerate increasing temperatures better than *Crematogaster* ants by moving deeper underground, into the thermally buffered chambers of their nests, to escape thermal stress (Włodarczyk, 2021). Such movement may cause pangolins to increase their digging activities in order to access underground prey, resulting in increased soil turnover. Hence, without further investigation to determine how pangolin prey genera may be affected by climate change, it is difficult to predict how the ecosystem services of pangolins may be altered.

If pangolins were to increase their digging activities it may increase the energetic cost of their foraging. It is likely energetically more costly to dig for prey (*Anoplolepis* ants) than to scratch and tear at bark (*Crematogaster* ants), so greater digging will increase the energy demands for pangolins. However, *Anoplolepis* ants are a higher energy food source (0.08 kJ and 0.02 kJ for *Anoplolepis* soldiers and workers, respectively) than *Crematogaster* ants (0.01 kJ; Panaino et al., 2022), which may balance the energetic costs of digging. Further research is needed to measure the energy investment of pangolins during foraging, by measuring the time spent at each type of foraging site, in an attempt to understand the energetic cost that changes in prey abundance and availability may have on pangolins. If the energetic cost of foraging were to increase, together with increased energetic and thermal stress as a result of climate change, this may result in the extirpation of pangolins (Panaino, 2021). In the Kalahari, aardvarks have been observed to die from starvation as a consequence of reduced grass cover causing a decline in their primary food source (termites; Weyer, 2018; Rey et al., 2017). A decline in pangolins would result in a decrease or loss of the ecosystem services that they provide, potentially leading to an overall reduction in ecosystem stability.

While my study has quantified some of the ecosystem services of Temminck's pangolins, namely, soil turnover, biodiversity accumulation and nutrient cycling, pangolins may provide additional services. Temminck's pangolins may modify the burrows created by other species, maintaining these burrows, and allowing the burrows to persist in the environment and to be utilised by other species (Sun et al., 2021). Through their foraging, Temminck's pangolins may alter plant community structure, via the increased accumulation of organic matter in dig sites elevating soil nutrient concentrations (Sun et al., 2021). Long-term research is needed to investigate whether pangolin dig sites promote seed germination, plant growth and plant species richness.

The pangolins used in my study inhabited the Gordonia Duneveld regions of the reserve; however, individuals also occur in the Koranna-Langeberg Mountain Bushveld. Pangolins occurring in the mountainous regions of the reserve have been observed to have different foraging behaviours (W. Panaino, personal communication), foraging more frequently on above-ground termite mounds as compared to digging for subterranean ants, as seen for their duneveld counterparts. My study did not investigate the foraging behaviour of these mountainous pangolins, and as far as I am aware, no ecological research has been conducted on pangolins in such a habitat. It is likely that the ecosystem services that pangolins in mountains provide, through soil turnover, biodiversity accumulation and nutrient cycling, are lower than those of duneveld pangolins.

Aardvarks, another fossorial species occurring in the Kalahari, are ecologically similar to pangolins. The aardvark is also a nocturnal species that feeds on ants and termites (Knöthig, 2005). Studies on aardvarks have shown that they are important ecosystem engineers, as their burrows have been recorded to be utilised by at least 21 mammal species (Whittington-Jones et al., 2011). Additionally, abandoned and collapsed aardvark burrows provide microclimate conditions that promote seedling growth, leading to elevated species richness as compared to the surrounding undisturbed area (Haussmann et al., 2018). Aardvarks have a much greater body mass, of 25 to 70 kg (Knöthig, 2005), than that of Temminck's pangolins (6 to 10 kg). The large body mass of aardvarks, together with strong clawed forelimbs, make them exceptional diggers (Knöthig, 2005), producing larger foraging digs than pangolins. However, no studies have investigated the soil turnover generated by aardvarks during foraging, nor the accumulation of biodiversity in their foraging digs. I speculate that the ecological contribution of aardvarks in the Kalahari, in terms of soil turnover and biodiversity accumulation, may be greater overall than that of pangolins, but may result in different impacts on biodiversity.

Temminck's pangolins have the widest distribution of all pangolin species, inhabiting a variety of habitats, such as arid savannas, thickets and woodlands (Challender et al., 2020). Temminck's pangolins have shown strong geographic prey selectivity (Challender et al., 2020), foraging predominantly on *Crematogaster* ants in the eastern dryland environments of South Africa (Panaino et al., 2022), in contrast to *Anoplolepis* ants in the northwestern savanna regions of the country (Swart et al., 1999). Hence, differences in the dominant prey species across the distribution of Temminck's pangolins may cause variation in foraging behaviour and, as a result, differences in the ecosystem services that pangolins provide.

While my study has contributed to the literature on the ecological role of Temminck's pangolins, little is known about the ecological role of other pangolin species, except for Chinese pangolins (Sun et al., 2021). The eight pangolin species have vastly different ecologies and as a result the ecosystem services that they provide likely differ. For example, giant pangolins feed predominantly on termites, digging for subterraneous colonies at depths of up to 50 cm (Challender et al., 2020). Therefore, the digging activities of giant pangolins likely translate to larger quantities of turned-over soil as compared to Temminck's pangolins. Black-bellied pangolins, an exclusively arboreal species, feed almost entirely on arboreal ant species, and therefore do not dig, but rather scratch and tear at bark to get to ant colonies (Challender et al., 2020). To fully understand the ecological impact of pangolin trafficking worldwide, research is required on the ecological role of all pangolin species.

While the ecological impact of losing pangolins and the ecosystem services they provide remains uncertain, pangolin trafficking has reached critical levels with an estimated 895 000 pangolins being trafficked between 2000 and 2019 (Challender et al., 2020). Historically, Asian pangolin species were primarily trafficked, however, between 2000 and 2019 there was a shift, with African species accounting for 65% (858 000 pangolins) of the global trade (Challender et al., 2020). This increase suggests that the conservation statuses of African pangolin species are at risk of changing to Endangered or Critically Endangered should this issue persist. For Temminck's pangolins, there is very little research on poaching across much of their range, including a lack of data on poaching in the Kalahari. This lack of poaching data makes it difficult to assess the full extent of the threat to Temminck's pangolins. However, the rising illegal trade in pangolins in southern Africa, driven by continued demand of the Asian market (Pietersen et al., 2014a; Challender et al., 2020), may lead to increased exploitation of Temminck's pangolins. Law enforcement determines appropriate punishment for those who participate in the illegal trafficking of a species by using legal frameworks that consider factors such as conservation status and the scale of the crime. However, understanding the ecological impact of poaching can serve as an additional tool to inform policies. Through scientists providing empirical evidence for the role that pangolins play in the ecosystem, law enforcement can make scientifically driven, evidence-based decisions regarding pangolin poaching cases. Examining the role of the Temminck's pangolin in the environment moves us one step closer to understanding what the loss of pangolins means to the ecosystem. My study has demonstrated, in part, the importance of pangolins in the ecosystem. An improved understanding of pangolin functional ecology will allow conservation organisations to appropriately prioritise the species through conservation assessments and allows law enforcement to apply appropriate punishment to criminals actively participating in removing species from ecosystems.

Raising awareness of the ecological role of pangolins may also better inform protection policies, by identifying critical regions that should be protected and factors that may impact the ecosystem services provided by pangolins. Better education on the ecological role of pangolins is needed, for example, to emphasise their importance to farmers (on whose properties pangolins may reside), as pangolins can contribute to the environment by increasing soil nutrients, soil turnover and accumulation of organic matter. Farmers may be prompted to become custodians of pangolins on their properties, aiding conservation efforts. By prioritising the ecological role of animals in conservation and promoting their ecosystem services, we can potentially reduce management inputs. For example, if apex predators are reintroduced into management areas, they control herbivore populations, which in turn promotes vegetation growth, as seen by the reintroduction of grey wolves (*Canis lupus*) to Yellowstone National Park (Ripple and Beschta, 2012). As a result, often the only external management required is at the top level, that of the apex predator. This form of management can potentially reduce conservation cost and promote ecosystem diversity, letting nature take care of nature. In the case of pangolin conservation, by conserving their ecological role of improved soil turnover, nutrient cycling and biodiversity accumulation, pangolins may promote vegetation growth, which may benefit herbivore species and, by extension, predators as well. Therefore, conserving a single species, Temminck's pangolins, may generate widespread benefits for the entire ecosystem.

Why care about the loss of pangolins?

The loss of pangolins represents not only a loss of a unique species, but also the loss of the essential ecosystems services they provide, negatively impacting the stability of the ecosystem.

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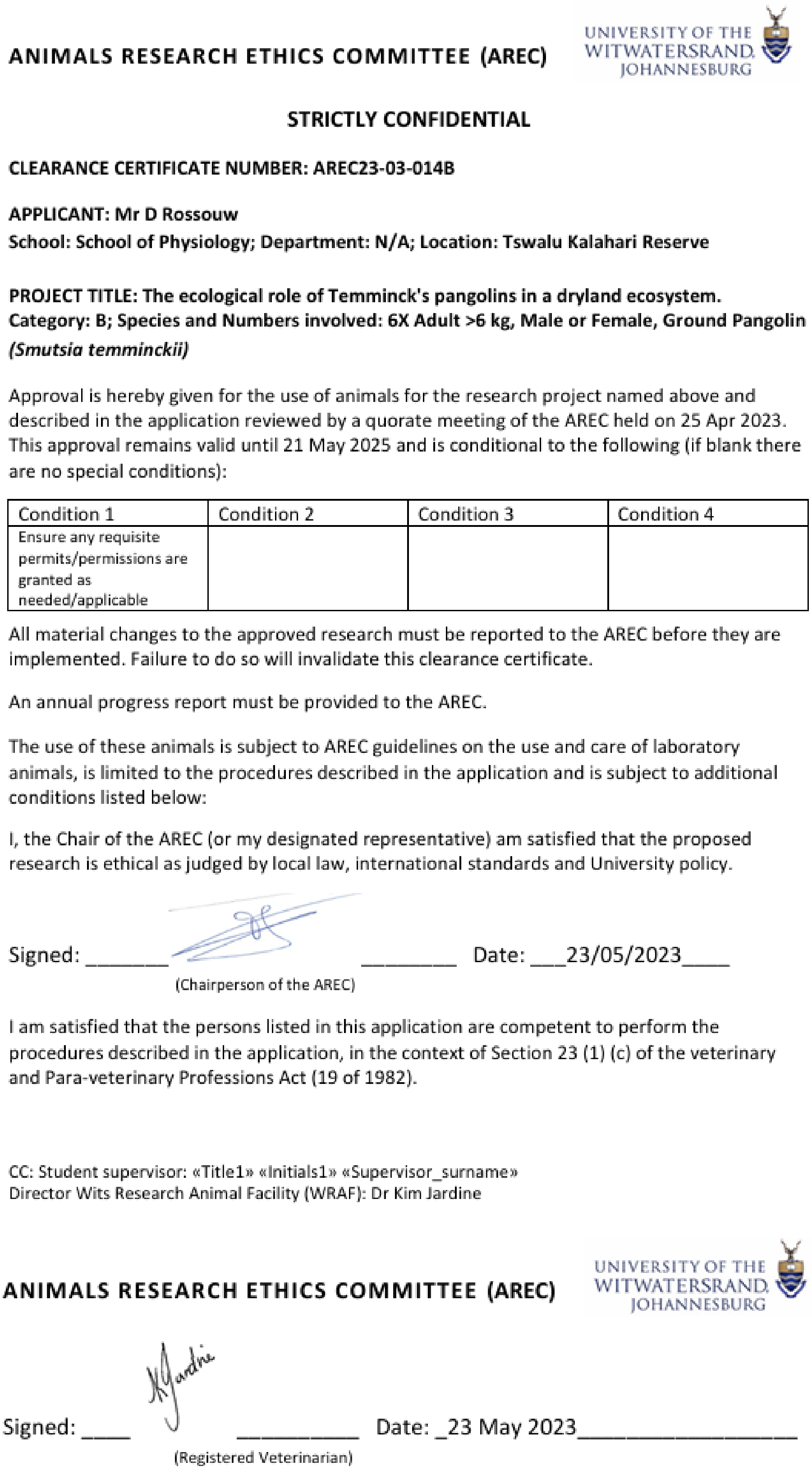
APPENDIX A

Ethical clearance certificate



ANIMALS RESEARCH ETHICS COMMITTEE (AREC)

UNIVERSITY OF THE
WITWATERSRAND,
JOHANNESBURG

STRICTLY CONFIDENTIAL

CLEARANCE CERTIFICATE NUMBER: AREC23-03-014B

APPLICANT: Mr D Rossouw
School: School of Physiology; Department: N/A; Location: Tswalu Kalahari Reserve

PROJECT TITLE: The ecological role of Temminck's pangolins in a dryland ecosystem.
Category: B; Species and Numbers involved: 6X Adult >6 kg, Male or Female, Ground Pangolin *(Smutsia temminckii)*

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 25 Apr 2023. This approval remains valid until 21 May 2025 and is conditional to the following (if blank there are no special conditions):

Condition 1	Condition 2	Condition 3	Condition 4
Ensure any requisite permits/permissions are granted as needed/applicable			

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: ___23/05/2023____

(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 Wits Research Animal Facility (WRAF): Dr Kim Jardine

ANIMALS RESEARCH ETHICS COMMITTEE (AREC)

UNIVERSITY OF THE
WITWATERSRAND,
JOHANNESBURG

Signed: ____ KJardine __________ Date: _23 May 2023_________________

(Registered Veterinarian)

APPENDIX B

Supplementary Tables

Chapter 1

Supplementary Table 1. Seasonal durations of the 24h above-ground active phase of pangolins in the Kalahari, as found by Panaino (2021).

Season	Duration (Mean ± SD)
Summer	07h00min ± 02h00min
Autumn	06h40min ± 01h47min
Winter	05h14min ± 01h25min
Spring	06h02min ± 02h25min
Average	6h16min ± 0h46min

Chapter 3

Supplementary Table 2. Statistical model descriptions for both pangolin foraging behaviour and prey abundance data, indicating the response variable, model type, fixed effect/predictor/grouping and random effect variables.

Response variable	Model type	Fixed effect/predictor/grouping variable	Random effect variable
		Pangolin foraging behaviour	
Foraging sites per hour	LMM (linear mixed effect model)	– Season	Pangolin individual
Distance foraged per hour (km)			
Proportion *Crematogaster* foraging sites			
Proportion *Anoplolepis* foraging sites			
log [foraging sites per hour +1]		– log [Distance foraged per hour + 1] (km)	
Sqrt [foraging sites per hour]		– Ants per trap (monthly average)	
Distance foraged per hour (km)	LM (linear model)		NA
Foraging sites per hour	T-test	– Observation session (hourly or full active phase)	NA
Distance foraged per hour (km)			
		Prey abundance	
Log [ants per trap + 1]	LM using generalized least squares	– Season – Air temperature – Rainfall	NA

Supplementary Table 3. AIC comparison between the linear mixed effect model and linear model for distance foraged with respects to prey abundance (ants per trap monthly average).

Response variable	Random effect variable (Pangolin individual)	AIC	Δ AIC
Distance foraged per hour (km) (n = 56)	Exclude (LM)	-62.64	0.00
	Included (LMM)	-42.77	-19.87

Supplementary Table 4. AIC comparison between the linear models using generalized least squares for prey abundance with varying monthly rainfall (current, 2 and 3 months prior).

Response variable	Monthly rainfall	AIC	Δ AIC
Log [ants per trap] (n = 315)	Current	792.94	0.00
	2 months prior	803.30	-10.36
	3 months prior	803.50	-10.56

Supplementary Table 5. Descriptive statistics for aspects of pangolin foraging behaviour, averaged across the year and across seasons.

Response variable	Season	Mean ± SD	Median	IQR	Range
Foraging sites per hour (n = 58)	Summer	17.9 ± 4.4	17.2	16.5 to 20.0	10.7 to 26.0
	Autumn	11.3 ± 6.3	12.5	4.8 to 17.1	2.0 to 21.5
	Winter	14.4 ± 9.7	13.1	8.2 to 18.9	1.0 to 32.0
	Spring	8.5 ± 3.9	8.0	5.1 to 11.7	3.6 to 16.0
	Average	12.5 ± 7.3	12.2	6.8 to 17.2	1.0 to 32.0
Response variable	**Season**	**Mean ± SD (km)**	**Median (km)**	**IQR (km)**	**Range (km)**
Distance foraged per hour (km) (n = 58)	Summer	0.3 ± 0.1	0.3	0.2 to 0.4	0.1 to 0.5
	Autumn	0.2 ± 0.2	0.2	0.1 to 0.3	<0.1 to 0.6
	Winter	0.2 ± 0.1	0.2	0.1 to 0.2	0.0 to 0.4
	Spring	0.3 ± 0.1	0.3	0.2 to 0.4	0.0 to 0.6
	Average	0.2 ± 0.1	0.2	0.1 to 0.3	0.0 to 0.6

Supplementary Table 6. Summary of linear mixed effect model results for various aspects of pangolin foraging behaviour.

Response variable	R^2_m	Fixed effect variable	β ± SE	95 % CI	df	t	p-value
Foraging sites per hour (n = 58)	0.17	Intercept	17.80 ± 2.33	13.15 to 22.25	5.09	7.63	<0.01
		Season (autumn)	-6.58 ± 2.74	-11.88 to -1.36	47.63	-2.40	<0.05
		Season (winter)	-3.38 ± 2.91	-8.93 to 2.27	6.75	-1.16	0.28
		Season (spring)	-9.26 ± 3.02	-15.06 to -3.27	6.77	-3.06	<0.05
	R^2_c	**Random effect variable**		**Variance ± SD**			
	0.18	Pangolin individual (n = 4)		0.31 ± 0.56			
		Residuals		46.28 ± 6.80			
Sqrt [foraging sites per hour] (n = 56)	0.03	Intercept	3.05 ± 0.35	2.43 to 3.75	1.38	8.77	0.04
		Ants per trap	0.01 ± 0.01	-0.01 to 0.03	1.31	1.03	0.46
	0.07	Pangolin individual (n = 4)		0.05 ± 0.23			
		Residuals		1.14 ± 1.07			
Distance foraged per hour (km) (n = 58)	0.08	Intercept	0.26 ± 0.06	0.14 to 0.39	8.08	4.20	<0.01
		Season (autumn)	-0.04 ± 0.06	-0.18 to 0.06	53.34	-0.74	0.47
		Season (winter)	-0.06 ± 0.07	-0.24 to 0.07	22.52	-0.91	0.37
		Season (spring)	0.05 ± 0.07	-0.14 to 0.19	25.75	0.69	0.50
	0.21	Pangolin individual (n = 4)		<0.01 ± 0.05			
		Residuals		0.02 ± 0.13			
Proportion *Crematogaster* foraging sites (n = 58)	0.30	Intercept	0.32 ± 0.16	-0.01 to 0.63	8.05	2.05	0.07
		Season (autumn)	0.24 ± 0.11	-0.01 to 0.45	53.53	2.12	0.04
		Season (winter)	0.04 ± 0.15	-0.33 to 0.33	48.08	0.25	0.80
		Season (spring)	0.58 ± 0.15	0.20 to 0.87	51.07	3.73	<0.01
	0.57	Pangolin individual (n = 4)		0.04 ± 0.20			

		Residuals	0.07 ± 0.26				
Proportion *Anoplolepis* foraging sites (n = 58)	0.27	Intercept	0.63 ± 0.17	0.31 to 0.98	7.98	3.66	<0.01
		Season (autumn)	-0.24 ± 0.12	-.046 to 0.01	53.33	-2.04	<0.05
		Season (winter)	-0.10 ± 0.16	-0.40 to 0.25	50.61	-0.63	0.53
		Season (spring)	-0.61 ± 0.16	-0.92 to -0.25	52.65	-3.79	<0.01
	0.59	Pangolin individual (n = 4)	0.05 ± 0.24				
		Residuals	0.07 ± 0.27				
Log [foraging sites per hour + 1] (n = 58)	0.21	Intercept	1.90 ± 0.18	1.56 to 2.24	10.99	10.71	<0.01
		log [Distance foraged per hour + 1] (km)	2.61 ± 0.67	1.31 to 3.93	55.80	3.89	<0.01
	0.27	Pangolin individual (n = 4)	0.02 ± 0.16				
		Residuals	0.31 ± 0.55				

Supplementary Table 7. Tukey's honestly significant difference seasonal pairwise comparison results for various aspect of pangolin foraging behaviour.

Response variable	**Pairwise comparison (season)**	**β ± SE**	**95 % CI**	**df**	**t**	**p-value**
Foraging sites per hour (n = 58)	Summer – autumn	6.58 ± 2.94	-1.25 to 14.41	46.83	2.24	0.13
	Summer – winter	3.38 ± 3.77	-9.69 to 16.45	5.99	0.90	0.81
	Summer – spring	9.26 ± 3.97	-4.48 to 22.99	6.00	2.33	0.19
	Autumn – winter	-3.20 ± 2.69	-10.84 to 4.45	16.83	-1.19	0.64
	Autumn – spring	2.68 ± 2.89	-5.53 to 10.88	17.40	0.93	0.79
	Winter – spring	5.88 ± 2.58	-0.96 to 12.71	53.94	2.28	0.12
Distance foraged per hour (km) (n = 58)	Summer – autumn	0.04 ± 0.06	-0.12 to 0.20	53.30	0.70	0.90
	Summer – winter	0.06 ± 0.08	-0.17 to 0.29	22.00	0.77	0.87
	Summer – spring	-0.05 ± 0.09	-0.29 to 0.19	25.20	-0.59	0.94
	Autumn – winter	0.02 ± 0.06	-0.14 to 0.18	32.30	0.38	0.98
	Autumn – spring	-0.09 ± 0.06	-0.26 to 0.07	39.20	-1.50	0.45
	Winter – spring	-0.11 ± 0.05	-0.25 to 0.02	53.90	-2.21	0.13
Proportion *Crematogaster* foraging sites (n = 58)	Summer – autumn	-0.24 ± 0.11	-0.54 to 0.07	53.50	-2.07	0.17
	Summer – winter	-0.04 ± 0.16	-0.48 to 0.40	47.90	-0.23	1.00
	Summer – spring	-0.58 ± 0.17	-1.02 to -0.14	51.00	-3.48	<0.01
	Autumn – winter	0.19 ± 0.12	-0.11 to 0.51	50.60	1.71	0.33
	Autumn – spring	-0.34 ± 0.12	-0.65 to -0.03	53.50	-2.87	<0.05
	Winter – spring	-0.54 ± 0.10	-0.81 to -0.27	53.20	-5.30	<0.01
Proportion *Anoplolepis* foraging sites (n = 58)	Summer – autumn	0.24 ± 0.12	-0.08 to 0.55	53.30	2.00	0.20
	Summer – winter	0.10 ± 0.17	-0.35 to 0.55	50.30	0.58	0.94
	Summer – spring	0.61 ± 0.17	0.16 to 1.07	52.50	3.57	<0.01
	Autumn – winter	-0.14 ± 0.12	-0.46 to 0.18	52.10	-1.14	0.67
	Autumn – spring	0.37 ± 0.12	0.05 to 0.70	53.90	3.07	<0.05
	Winter – spring	0.51 ± 0.11	0.23 to 0.79	53.00	4.86	<0.01

Supplementary Table 8. Seasonal pairwise comparison results, without adjustment for multiple comparisons, for pangolin foraging frequency.

Response variable	**Pairwise comparison (season)**	**β ± SE**	**95 % CI**	**df**	**t**	**p-value**
Foraging sites per hour (n = 58)	Summer – autumn	6.58 ± 2.94	0.66 to 12.49	46.83	2.24	0.03
	Summer – winter	3.38 ± 3.77	-5.86 to 12.62	5.99	0.90	0.41
	Summer – spring	9.26 ± 3.97	-0.46 to 18.97	6.00	2.33	0.06
	Autumn – winter	-3.20 ± 2.69	-8.87 to 2.47	16.83	-1.19	0.25
	Autumn – spring	2.68 ± 2.89	-3.42 to 8.77	17.40	0.93	0.37
	Winter – spring	5.88 ± 2.58	0.71 to 11.04	53.94	2.28	0.03

Supplementary Table 9. Summary of linear model results of pangolin foraging distance in relation to prey abundance (ants per trap monthly average), and prey abundance (log [ants per trap]) across seasons.

Response variable	**R^2**	**Fixed effect variable**	**β ± SE**	**95 % CI**	**df**	**t**	**p-value**
Distance foraged per hour (km) (n = 56)	0.14	Intercept	0.15 ± 0.03	0.08 to 0.22	54	4.34	<0.01
		Ants per trap	<0.01 ± <0.01	<0.01 to 0.01	54	3.15	<0.01
Log [ants per trap] (n = 315)	0.34 (pseudo)	Intercept	0.71 ± 0.54	-0.35 to 1.78	309	1.32	0.19
		Season (autumn)	-0.14 ± 0.23	-0.59 to 0.31	309	-0.62	0.54
		Season (winter)	-0.33 ± 0.34	-0.99 to -0.33	309	-0.97	0.33
		Season (spring)	-0.91 ± 0.22	-1.33 to -0.48	309	-4.18	<0.01
		Monthly rainfall	-0.02 ± 0.01	-0.03 to -0.01	309	-4.27	<0.01
		Monthly average temperature	0.11 ± 0.02	0.08 to 0.15	309	-6.40	<0.01

Supplementary Table 10. Descriptive statistics for non-logged pangolin prey abundance (ants per trap), averaged across the year and across seasons.

Response variable	Season	Mean ± SD	Median	IQR	Range
Ants per trap (n = 315)	Summer	28.7 ± 23.2	14.6	13.1 to 39.9	0.3 to 97.6
	Autumn	27.0 ± 28.1	9.5	6.7 to 32.7	0.9 to 95.6
	Winter	13.7 ± 17.3	21.0	3.2 to 16.9	0.4 to 82.2
	Spring	13.4 ± 13.1	6.8	4.4 to 17.4	0.7 to 76.5
	Average	19.4 ± 21.4	11.7	5.0 to 26.6	0.3 to 97.6

Supplementary Table 11. Tukey's honestly significant difference seasonal pairwise comparison results for pangolin prey abundance (log [ants per trap]) across seasons.

Response variable	Pairwise comparison (season)	β ± SE	95 % CI	df	t	p-value
Log [ants per trap] (n = 315)	Summer – autumn	0.14 ± 0.23	-0.47 to 0.75	50.10	0.62	0.93
	Summer – winter	0.33 ± 0.34	-0.56 to 1.22	62.00	0.97	0.77
	Summer – spring	0.91 ± 0.22	0.33 to 1.49	39.30	4.18	<0.01
	Autumn – winter	0.19 ± 0.22	-0.40 to 0.77	65.70	0.85	0.83
	Autumn – spring	0.77 ± 0.16	0.33 to 1.20	48.30	4.73	<0.01
	Winter – spring	0.59 ± 0.22	-0.01 to 1.16	51.60	2.65	0.05

Chapter 4

Supplementary Table 12. Statistical model descriptions for pangolin foraging measures (soil turnover, nutrient cycling and biodiversity accumulation), indicating the response variable, model type, fixed effect/grouping and random effect variables.

Response variable	**Model type**	**Fixed effect variables/grouping variable**	**Random effect variable**
		Soil turnover	
Soil turnover per dig site (kg)	Kruskal-Wallis test	– Season	NA
Soil turnover per dig site (kg)	Spearman's Rank Correlation test	– Ants per trap (seasonal average)	
		Biodiversity accumulation	
Log [accumulated organic matter per dig site + 1] (g)	LMM	– Sample month (1, 4, 7, 10 months post foraging event)	Pangolin individual
Dig width (cm)	Kruskal-Wallis test		NA
Dig length (cm)			
		Nutrient cycling	
Nitrogen concentration (%)	LM	– Sample type (dig site or control sites)	NA
Sqrt [total carbon concentration + 0.03] (%)	LM using generalized least squares	– Sample month (0, 3, 6, 9 months post foraging event)	
Nitrogen concentration (%) (subset with dig sites only)	LM	– Sample month (0, 3, 6, 9 months post foraging event)	NA
Sqrt [total carbon concentration + 0.03] (%) (subset with dig sites only)	LM using generalized least squares		

Supplementary Table 13. AIC comparison between the linear models and linear mixed effect models for nutrient cycling.

Response variable	Random effect variable (Pangolin individual)	AIC	Δ AIC
Nitrogen concentration (%)	Exclude (LM)	-763.14	0.00
	Included (LMM)	-706.95	-56.19
Nitrogen concentration (%) (subset with dig sites only)	Exclude (LM)	-375.85	0.00
	Included (LMM)	-333.44	-42.41

Supplementary Table 14. Descriptive statistics for the soil turnover generated per dig site by pangolins, averaged across the year and across seasons.

Response variable	Season	Mean ± SD (kg)	Median (kg)	IQR (kg)	Range (kg)
Soil turnover per dig site (kg) (n = 200)	Summer	0.7 ± 0.6	0.5	0.2 to 1.0	<0.1 to 2.5
	Autumn	0.8 ± 1.5	0.5	0.2 to 0.8	<0.1 to 10.0
	Winter	2.8 ± 2.3	1.9	1.2 to 4.0	0.5 to 10.8
	Spring	2.0 ± 2.4	1.1	0.7 to 2.1	0.1 to 10.2
	Average	1.6 ± 2.0	0.9	0.4 to 1.9	<0.1 to 10.8

Supplementary Table 15. Dunn's seasonal pairwise comparison results for soil turnover generated per dig site by pangolins.

Response variable	Pairwise comparison (season)	Z	Adjusted p-value
Soil turnover per dig site (kg) (n = 200)	Autumn – spring	-4.51	<0.01
	Autumn – summer	-0.31	1.00
	Autumn – winter	-7.06	<0.01
	Spring – summer	4.21	<0.01
	Spring – winter	-2.55	0.06
	Summer – winter	-6.75	<0.01

Supplementary Table 16. Summary of linear mixed effect model results for biodiversity accumulation with respects to time post pangolin foraging event (sample month)

Response variable	**R^2_m**	**Fixed effect variable**	**β ± SE**	**95 % CI**	**df**	**t**	**p-value**
Log [accumulated organic matter per dig site + 1] (g) (n = 79)	0.02	Intercept	1.64 ± 0.17	1.32 to 1.95	10.83	9.81	<0.01
		Sample month (4)	0.16 ± 0.22	-0.26 to 0.59	73.09	0.74	0.46
		Sample month (7)	-0.11 ± 0.22	-0.53 to 0.32	73.09	-0.48	0.63
		Sample month (10)	-0.05 ± 0.3	-0.50 to 0.39	73.52	-0.22	0.83
	R^2_c	**Random effect variable**		**Variance ± SD**			
	0.05	Pangolin individual (n = 3)		0.01 ± 0.12			
		Residuals		0.50 ± 0.71			

Supplementary Table 17. Descriptive statistics for the change in pangolin dig width and dig depth as time post foraging event (sample month) increased and averaged across the year.

Response variable	**Sample month (months post foraging event)**	**Mean ± SD (cm)**	**Median (cm)**	**IQR (cm)**	**Range (cm)**
Dig width (cm) (n = 60)	1	22.5 ± 3.9	20.5	20.3 to 23.8	20.0 to 27.0
	4	18.3 ± 3.5	18.3	16.4 to 20.5	11.5 to 26.0
	7	15.9 ± 5.2	15.8	14.0 to 19.5	0.0 to 22.5
	10	20.1 ± 9.9	18.0	15.0 to 24.0	0.0 to 42.0
	Average	18.3 ± 6.6	18.0	15.4 to 20.8	0.0 to 42.0
Dig depth (cm) (n = 60)	1	9.7 ± 3.1	9.0	8.0 to 11.0	7.0 to 13.0
	4	6.9 ± 3.9	6.3	5.4 to 7.0	2.0 to 21.0
	7	4.9 ± 5.1	4.0	2.8 to 4.6	0.0 to 25.0
	10	5.7 ± 4.1	4.5	3.5 to 5.5	0.0 to 15.5
	Average	6.0 ± 4.4	5.0	3.9 to 7.0	0.0 to 25.0

Supplementary Table 18. Dunn's pairwise comparison results for pangolin dig width and dig depth with respects to time post pangolin foraging event (sample month)

Response variable	Pairwise comparison (season)	Z	Adjusted p-value
Dig width (cm) (n = 60)	Sample month (1) – (4)	1.26	1.00
	Sample month (1) – (7)	2.11	0.21
	Sample month (1) – (10)	1.20	1.00
	Sample month (4) – (7)	1.67	0.57
	Sample month (4) – (10)	-0.07	1.00
	Sample month (7) – (10)	-1.68	0.56
Dig depth (cm) (n = 60)	Sample month (1) – (4)	1.22	1.00
	Sample month (1) – (7)	2.76	0.03
	Sample month (1) – (10)	2.28	0.14
	Sample month (4) – (7)	3.01	0.02
	Sample month (4) – (10)	2.04	0.25
	Sample month (7) – (10)	-0.84	1.00

Supplementary Table 19. Summary of linear model results for nutrient cycling with respects to time post pangolin foraging event (sample month).

Response variable	R^2	Fixed effect variable	β ± SE	95 % CI	df	t	p-value
Nitrogen concentration (%) (n =120)	0.44	Intercept	0.04 ± <0.01	0.04 to 0.05	115	22.17	<0.01
		Sample type (control)	<0.01 ± <0.01	<-0.01 to <0.01	115	0.22	0.83
		Sample month (3)	-0.01 ± <0.01	-0.01 to <-0.01	115	-2.59	0.01
		Sample month (6)	-0.02 ± <0.01	-0.03 to -0.02	115	-9.03	<0.01
		Sample month (9)	-0.02 ± <0.01	-0.02 to -0.01	115	-6.73	<0.01
Sqrt [total carbon concentration + 0.03] (%) (n =120)	0.87 (pseudo)	Intercept	0.41 ± 0.01	0.39 to 0.44	115	31.73	<0.01
		Sample type (control)	-0.02 ± 0.01	-0.04 to <0.01	115	-1.95	0.05
		Sample month (3)	0.11 ± 0.01	0.09 to 0.13	115	9.13	<0.01
		Sample month (6)	0.09 ± 0.01	0.07 to 0.12	115	6.86	<0.01
		Sample month (9)	0.06 ± 0.01	0.03 to 0.09	115	4.59	<0.01
Nitrogen concentration (%) (n = 60) (subset with dig sites only)	0.39	Intercept	0.04 ± <0.01	0.04 to 0.05	56	16.75	<0.01
		Sample month (3)	-0.01 ± <0.01	-0.01 to <0.01	56	-1.50	0.14
		Sample month (6)	-0.02 ± <0.01	-0.03 to -0.01	56	-5.74	<0.01
		Sample month (9)	-0.02 ± <0.01	-0.02 to -0.01	56	-4.19	<0.01
Sqrt [total carbon concentration + 0.03] (%) (n = 60) (subset with dig sites only)	0.87 (pseudo)	Intercept	0.40 ± 0.02	0.36 to 0.44	56	19.53	<0.01
		Sample month (3)	0.12 ± 0.02	0.09 to 0.16	56	7.60	<0.01
		Sample month (6)	0.11 ± 0.02	0.07 to 0.15	56	6.04	<0.01
		Sample month (9)	0.07 ± 0.02	0.03 to 0.11	56	3.70	<0.01

Supplementary Table 20. Descriptive statistics for the change in nitrogen and total carbon concentration in pangolin dig sites as time post foraging event (sample month) increased and averaged across the year.

Response variable	Sample month (months post foraging event)	Mean ± SD (%)	Median (%)	IQR (%)	Range (%)
Nitrogen concentration (%) (n = 60) (subset with dig sites only)	0	0.04 ± 0.01	0.04	0.03 to 0.05	0.02 – 0.06
	3	0.04 ± 0.01	0.03	0.03 to 0.05	0.02 – 0.06
	6	0.02 ± 0.01	0.02	0.02 to 0.03	0.01 – 0.04
	9	0.03 ± 0.01	0.03	0.02 to 0.03	0.01 – 0.05
	Average	0.03 ± 0.01	0.03	0.02 to 0.04	0.01 – 0.06
Total carbon concentration (%) (n = 60) (subset with dig sites only)	0	0.13 ± 0.06	0.12	0.09 to 0.16	0.06 – 0.30
	3	0.25 ± 0.05	0.24	0.23 to 0.28	0.17 – 0.35
	6	0.24 ± 0.05	0.24	0.20 to 0.28	0.16 – 0.34
	9	0.20 ± 0.07	0.19	0.17 to 0.20	0.11 – 0.36
	Average	0.20 ± 0.07	0.20	0.16 to 0.25	0.06 – 0.36

Supplementary Table 21. Tukey's honestly significant difference pairwise comparison results for biodiversity accumulation and nutrient cycling with respects to time post pangolin foraging event (sample month).

Response variable	Pairwise comparison (sample month)	β ± SE	95 % CI	df	t	p-value
Log [accumulated organic matter per dig site + 1] (g) (n = 79)	Sample month (1) – (4)	-0.16 ± 0.22	-0.74 to 0.41	73.20	-0.74	0.88
	Sample month (1) – (7)	0.11 ± 0.22	-0.47 to 0.68	73.20	0.48	0.96
	Sample month (1) – (10)	0.05 ± 0.23	-0.56 to 0.65	73.60	0.21	1.00
	Sample month (4) – (7)	0.27 ± 0.22	-0.32 to 0.86	73.00	1.19	0.63
	Sample month (4) – (10)	0.21 ± 0.23	-0.40 to 0.83	73.20	0.90	0.80
	Sample month (7) – (10)	-0.06 ± 0.23	-0.67 to 0.56	73.20	-0.24	1.00
Nitrogen concentration (%) (n =120)	Sample month (0) – (3)	0.01 ± <0.01	<-0.01 to 0.01	115	2.59	0.05
	Sample month (0) – (6)	0.02 ± <0.01	0.02 to 0.03	115	9.03	<0.01
	Sample month (0) – (9)	0.02 ± <0.01	0.01 to 0.02	115	6.75	<0.01
	Sample month (3) – (6)	0.02 ± <0.01	<0.01 to 0.02	115	6.34	<0.01
	Sample month (3) – (9)	0.01 ± <0.01	<0.01 to 0.02	115	4.12	<0.01
	Sample month (6) – (9)	-0.01 ± <0.01	-0.01 to <0.01	115	-2.11	0.16
Sqrt [total carbon concentration + 0.03] (%) (n =120)	Sample month (0) – (3)	-0.11 ± 0.01	-0.14 to -0.09	42.20	-9.14	<0.01
	Sample month (0) – (6)	-0.09 ± 0.01	-0.13 to -0.06	53.40	-6.86	<0.01
	Sample month (0) – (9)	-0.06 ± 0.01	-0.10 to -0.03	49.10	-4.59	<0.01

	Sample month (3) – (6)	0.02 ± 0.01	-0.01 to 0.04	46.50	1.81	0.28
	Sample month (3) – (9)	0.05 ± 0.01	0.02 to 0.08	50.60	4.43	<0.01
	Sample month (6) – (9)	0.03 ± 0.01	<0.01 to 0.06	47.80	3.02	0.02
Nitrogen concentration (%) (n = 60) (subset with dig sites only)	Sample month (0) – (3)	0.01 ± <0.01	<-0.01 to 0.01	56	1.50	0.44
	Sample month (0) – (6)	0.02 ± <0.01	0.01 to 0.03	56	5.74	<0.01
	Sample month (0) – (9)	0.02 ± <0.01	0.01 to 0.03	56	4.19	<0.01
	Sample month (3) – (6)	0.02 ± <0.01	0.01 to 0.03	56	4.18	<0.01
	Sample month (3) – (9)	0.01 ± <0.01	<0.01 to 0.02	56	2.67	0.05
	Sample month (6) – (9)	-0.01 ± <0.01	-0.02 to <0.01	56	-1.43	0.49
Sqrt [total carbon concentration + 0.03] (%) (n = 60) (subset with dig sites only)	Sample month (0) – (3)	-0.12 ± 0.02	-0.17 to -0.08	16.70	-7.60	<0.01
	Sample month (0) – (6)	-0.11 ± 0.02	-0.16 to -0.06	24.50	-6.04	<0.01
	Sample month (0) – (9)	-0.07 ± 0.02	-0.12 to -0.02	27.10	-3.70	<0.01
	Sample month (3) – (6)	0.01 ±0.01	-0.02 to 0.05	22.70	1.17	0.65
	Sample month (3) – (9)	0.06 ± 0.02	<0.01 to 0.11	15.40	2.96	0.04
	Sample month (6) – (9)	0.04 ± 0.02	-0.01 to 0.09	16.90	2.43	0.11

Supplementary Table 22. Seasonal and yearly estimates of soil turnover generated by a single pangolin individual.

Variable	**Season**	**Mean ± SD (kg)**
Soil turnover per dig site (kg) (n = 200)	Summer	2 399 ± 2 773
	Autumn	1 385 ± 2 194
	Winter	10 568 ± 9 983
	Spring	1 267 ± 2 054
	Yearly	15 619 ± 10 788

Supplementary Table 23. Seasonal and yearly estimates of foraging sites of a single pangolin individual, overall and for the two main prey genera of pangolins.

Variable	**Season**	**Mean ± SD**
Foraging sites	Summer	11 515 ± 4 351
	Autumn	6 837 ± 4 256
	Winter	6 784 ± 4 918
	Spring	4 719 ± 2 709
	Yearly	29 855 ± 8 281
Crematogaster foraging sites	Summer	6 644 ± 3 122
	Autumn	4 518 ± 2 505
	Winter	1 707 ± 1 424
	Spring	3 686 ± 1 258
	Yearly	16 554 ± 4 431
Anoplolepis foraging sites	Summer	4 385 ± 3 358
	Autumn	2 171 ± 2 520
	Winter	4 527 ± 2 074
	Spring	887 ± 1 171
	Yearly	11 971 ± 4 827

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Supplementary Table 24. Estimates of biodiversity accumulation (organic matter) in dig sites created by a single pangolin produces across a year, at different times post dig event (sample month), including the yearly average.

Variable	Sample month (months post foraging event)	Mean ± SD (kg)
Accumulated organic matter per dig site (g)	1	69.5 ± 72.0
	4	80.1 ± 75.4
	7	54.7 ± 46.4
	10	59.4 ± 53.2
	Yearly	66.1 ± 62.8