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Variation in aardvark (*Orycteropus afer*) burrow use between natural and agricultural sites in the Bronkhorstspruit-Middelburg region, South Africa

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Plagiarism Declaration

I, Jordan Izabella Netherlands declare that the dissertation which I hereby submit for the degree Master of Science in Environmental Ecology at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature:

Date: 1 December 2022

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Abstract

Aardvark (*Orycteropus afer*) burrows provide shelter to a variety of organisms, making it important to understand how these engineered environments get utilized in areas that are affected by agricultural activities. To address this, camera traps were used to record the use of abandoned aardvark burrows by other species at two sampling sites in the Bronkhorstspruit-Middelburg region in South Africa: a natural site (Telperion Nature Reserve) and a transformed site (pastoral fields of a grain farm and grazing paddocks). Data from traps placed in front of 36 burrows over a five-week period were analysed in R-Studio using generalized Linear Models (GLMs), Generalized Linear Mixed Models (GLMMs) and Chi-square tests to test whether there were any differences in the response variables between Telperion and the farm. Response variables included species richness, encounter frequency, burrow proximity, activity duration and activity times. In total 37 species were observed throughout the study of which 13 species were found at both sites, specifically nine mammal and four bird species. Whilst no statistically significant difference in species richness was found, differences in spatial dispersion between sites were observed for some species, possibly due to habitat preferences and/or human activities. Furthermore, the results of encounter frequency show that some species occur more frequently at Telperion, while others occur more frequently at the farm, possibly due to historical hunting and current poaching at the farm, in combination with habitat sensitivity and resource availability. Although no notable differences in activity times and duration were found for any of the species between sites, some species showed slight alterations in how they spent their time at the burrows which suggests that agricultural activity may have a minimal impact on these aspects of species behaviour. The results confirm that aardvark burrows may provide shelter, and foraging opportunities for numerous species living within agricultural environments in this region and highlight the conservation opportunities that these spaces represent. Efforts and funding to preserve keystone species, such as aardvark, and the burrows they engineer, should incorporate both farming and protected settings to be effective.

Keywords

Aardvark, ecosystem engineer, keystone species, grassland, burrow dwelling species, agriculture

List of figures

List of tables

Table of Contents

1. General Introduction

Grasslands across the world provide resources for many wildlife species yet are rapidly being transformed to land more suited for agricultural activities, such as livestock grazing and crop production (Carbutt et al. 2011). With habitat loss, fragmentation, and other potential threats, grasslands have become critically endangered and are considered one of the most threatened biomes in the world (Reyers et al. 2001, Newbold et al. 2016). These transformed areas may have significant impacts on the processes and pathways of activity of many wildlife species. Keystone species, that play a large role in the functioning of a community, need to be conserved in such environments to ensure that no negative cascading effects are seen throughout the community (Mills et al. 1993). This study examines the role that burrows created by a significant keystone species, the aardvark (*Orycteropus afer*), play in a grassland landscape that has been transformed into crop lands and grazing paddocks for livestock.

1.1. The role of burrowing mammals as ecosystem engineers and keystone species

Shelter, food, and water are three critical elements within the environment that animals rely on for survival (Krebs 1985). Various animals have different adaptations to get these elements and optimize their environment. Animals that modify, maintain, and create habitats, which facilitate a niche environment, directly or indirectly, for the survival of other organisms are known as ecosystem engineers (Smithers 1971, Jones et al. 1994, Mahan 2009, Whittington-Jones et al. 2011, Osborne 2016). The majority of ecosystem engineers can be grouped into burrowers, nest-builders, and herbivores with structural impacts, whereas the rest are grouped as soil-manipulators, leaf-structurers and organisms that are responsible for other trophic interactions (Coggan et al. 2018). An example of burrowing engineers are mole-rats (*Bathyergidae* spp.), where subterranean mole-rats of the family Bathyergidae modify the physical and chemical properties of soil, impacting the dynamics of plant communities (Hagenah & Bennett, 2013). An example of an herbivorous engineer is the African bush elephant (*Loxodonta Africana*) since they damage trees in savannah ecosystems and by doing so provide refuge for other vertebrates, such as lizards that prefer to use elephant-damaged trees as nests (Pringle 2008).

One adaptation that some ecosystem engineers have that enables animals to have access to shelter, is the ability to create burrows for protection from predators and temperature extremes (Schmidt-Nielson & Schmidt-Nielson 1950), as well as for denning and foraging (Kinlaw 1999). The burrows provide protection from the elements by creating a stable internal temperature range, known as a buffered microclimate (Kinlaw 1999). These microclimates allow the burrow occupant to cope in relation to seasonal and daily temperature cycles by maintaining a stable body temperature (Taylor & Skinner 2003, Pike & Mitchell 2013). In addition, burrows have also been shown to increase the abundance and diversity of plants and insects nearby (Davidson et al. 2012). However, not all animals can dig their own burrows and some therefore have to rely on other burrow digging animals.

Kinlaw (1999) broadly classified burrowing animals into three categories, namely ‘primary excavators’, ‘secondary modifiers’ and ‘simple dwellers’. Primary excavators include all animals that can dig their own burrows. Examples include aardvark (Melton 1976) and spring hare (*Pedetes capensis;* Butynski & Mattingly 1979). Animals that occupy burrows created by primary excavators and that further transform the burrow are secondary modifiers. Examples include porcupines (Alkon 1999), ground pangolins (Jacobsen et al. 1991) and common warthogs (*Phacochoerus africanus;* Sowls and Phelps 1966). Animals that simply take advantage of pre-excavated burrows, without further altering the burrow are the simple dwellers. Examples of simple dwellers include mammals such as steenbok (*Raphicerus campestris*), small rodents, birds such as blue swallows (*Hirundo atrocaerulea*), reptiles such as ground agamas and snakes, and amphibians such as toads (Whittington-Jones et al. 2011). The primary excavators, by creating moderated abiotic conditions and providing refuge opportunities to a wide range of other species, are all ecosystem engineers. The burrows excavated by these ecosystem engineers are an important resource for vertebrates globally, with the recorded number of species ranging from 64 species for prairie dog (*Cynomys* spp.) burrows (Campbell & Clarke 1981), 27 species for aardvark burrows (Whittington-Jones et al. 2011), 14 species for kangaroo rat (*Diodomys* spp.) burrows (Hawkins & Nicoletto 1992), eight species for European badger (*Meles meles*) burrows (Mori et al. 2014), and seven species for spring hare burrows (Smithers 1971).

Both the aardvark and the spring hare are classified as ecosystem engineers; however, they can also be termed keystone species or keystone modifiers due to the cascading effects they have within environments (Kinlaw 1999, Whittington Jones 2006, Butynski 2013, Haussmann et al. 2018). Species that play a positive role in community organization, the ecological functioning of a community, as well as the abundance and occurrence of other species are known as keystone species (Paine 1969, Mills et al. 1993). Wright and Jones (2006) distinguish keystone species from ecosystem engineers based on the outcomes of certain behaviours and ecological processes, rather than placing emphasis on the ecological processes itself; some species however can fall within both categories. An example of a keystone species is the North American beaver (*Castor canadensis*), which has a significant impact on the hydrology and productivity of the area due to the dams that it builds (Naiman et al. 1986). Another example is the Brazilian termite (*Cornitermes cumulans*), as the mounds that it builds are used by many other species and are critical for their survival (Redford 1984). Similarly, termites of the *Macrotermes* genus build large mounds in African woodlands, which allow for ecosystem heterogeneity due to the increased vegetation surrounding the burrows as well as their provision of habitat to a variety of burrowing mammals (Fleming & Loveridge 2003). Keystone species have a relatively large sphere of influence on a community, and therefore many scientists advocate for conservation efforts to be targeted towards them to ensure the continued support of other co-occurring species (Simberloff 1998, Caro and O'Doherty 1999, Jordán 2009). However, although keystone species are important within ecosystems, studies demonstrating the positive impact that they have on environments following reintroduction, are generally lacking (Hale & Koprowski 2018).

1.2. The aardvark as an ecosystem engineer and keystone species

Aardvarks are large, solitary, nocturnal mammals, with a unique pig-like appearance that share dietary similarities with pangolins (Manidae) and South American anteaters (Myrmecophagidae) (van Aarde 2004). They are obligate myrmecophages with a diet consisting of ants and termites, which they obtain using their elongated mouth and long tongue (Melton 1976). The aardvark has a large body, arched back, long muscular tail and head tapering into a snout, in addition to strong fore legs with powerful sharp claws that are well adapted for digging (van Aarde 2004). Aardvarks previously ranged throughout Africa during the Palaeocene, and in western Australia and southern Europe, from the middle Miocene (Melton 1976, Rahm 1990, Shoshani 2002). However, their current distribution is restricted to sub-Saharan Africa (Skinner & Smithers 1990). Their habitat includes open grass, scrub, and woodland in southern Africa, as well as forests in central and West Africa (Skinner & Smithers 1990). They are generally found in areas near termite mounds, since that is their main prey source, and this may contribute to their patchy distribution (Kingdon 1971, Melton 1975).

Aardvarks dig three types of burrows, namely for food or foraging, temporary refuge, and permanent residence (Smithers 1971). Food or foraging burrows do not go deep enough into the soil surface to fit the entire animal, whereas temporary burrows, although generally shallower than permanent burrows, consist of a single sleeping chamber (Smithers 1971). Although they fit an entire animal, temporary burrows are smaller than permanent burrows which are deeper, and more complex, with various chambers and tunnels within the burrow that, when abandoned, provide refuge to other species (Smithers 1971, Melton 1976, Skinner & Smithers 1990). Aardvark burrows are abundant in certain landscapes and remain in the environment for an extended period. They are also complex systems, allowing a variety of animals to use the burrows, by sharing them or using them solely for themselves (Taylor & Skinner 2003, Whittington-Jones et al. 2011).

In arid and mesic thicket environments, 27 vertebrate species have been recorded using aardvark burrows, including various mammal, bird, reptile, and amphibian species (Hockey et al. 2005, Whittington-Jones et al. 2011). Examples of simple dwellers, i.e. species simply using burrows, include spotted hyaena (*Crocuta Crocuta*), common warthog, aardwolf (*Proteles cristata*), various mongoose species, black-footed cats (*Felis nigreps*), African wild-dogs (*Lycaon pictus*) and Temminck's ground pangolin (*Smutsia temminckii*) (Sheppe & Osborne 1971, White 2007, Shackleton et al. 2018). Warthog and Cape porcupine (*Hystrix africaeaustralis*), on the other hand, can either use abandoned aardvark burrows as they are, making them simple dwellers, or they can modify them further, making them secondary modifiers (Cumming, 1975, Skinner and Smithers 1990). Cape porcupine have also been recorded sharing burrows with warthogs and hyaenas (Mills & Haagner 1989, Knothig 2005). Furthermore, certain bird species that use aardvark burrows for nesting and shelter can also be classified as secondary modifiers (Cilliers 2002, Hockey et al. 2005). Blue swallows construct their nests in a variety of landscapes such as, riverbanks, mine shafts, sink holes, and aardvark burrows (Keith et al. 1992, Combrink & Little 2012, Wakelin et al. 2013). However, in Whittington-Jones' study (2011), only ant-eating chats were frequently observed.

As demonstrated in gopher tortoises (*Gopherus polyphemus*), the burrows provide a buffered microhabitat, allowing occupants to maintain a stable body temperature throughout the day and avoid temperature extremes (Pike & Mitchell 2013, Louw et al. 2017). Maximum internal burrow temperatures within aardvark burrows in hot, arid regions, such as the Kalahari, in South Africa, are significantly lower than that of ambient temperatures, while humidity and minimum temperatures are higher, thereby significantly reducing the thermoregulatory costs to inhabitants (Whittington-Jones et al. 2011, Louw et al. 2017). In less arid environments, external temperature fluctuations are not as drastic, yet still occur. For example, warthogs overnight in aardvark burrows for thermo-regulatory reasons, to avoid hypothermia, since they do not cope well with low temperatures (Sowls and Phelps 1966, Cumming 1975, Estes 1991). In addition to this, burrows are also used as a protection mechanism from predators. At night, when the risk of predation is higher, warthogs retreat to their burrows away from predators (le Roux et al. 2018). In addition to the shelter and refuge opportunities that aardvark burrows provide to a variety of species, they have also been shown to influence food gathering and storage of certain species (Kinlaw 1999). Some organisms, such as the pouched mouse (*Saccostomus campestris*), store food for future consumption, known as food hoarding, which allows them the benefit of a broader diet (Reichman & Fay 1983, Smith & Reichman 1984). Furthermore, Cape porcupine have been shown to increase the seedlings found close to burrows due to their digging and soil turnover capabilities, thereby increasing the resources available to other organisms (Alkon 1999, Bragg et al. 2005).

Due to the significant influence that aardvark burrows have on other species in an area, it is crucial to understand how they might be affected by anthropogenic change, such as habitat transformation and land degradation, to understand how the broader ecological community might also be affected. The aardvark was categorized as being of 'least concern' on the IUCN Red List in 2015 (Taylor & Lehmann 2015), however its current status is unknown. Habitat loss, climate change, hunting for bushmeat, as well as poaching, pose a threat to this species (Melton 1976; Rey et al. 2017). In hotter areas, such as the Kalahari, increasing temperatures are leading to a decrease in ants and termites for aardvarks, and consequently a reduction in aardvark numbers, which will have significant top-down effects on all the animals that rely on aardvark burrows in that region (Rey et al. 2017). The effects of agricultural activity, and associated habitat transformation, on burrowing mammals and burrow ecology have not been thoroughly studied. Given the ever-increasing human population (UN 2019) and consequent agricultural expansion (Ritchie and Roser 2013), this information would be useful in conservation efforts focussed not only of the burrower itself, but also on species that rely on aardvark burrows for survival since there may be clear cascading effects resulting from the loss of aardvarks.

1.3. Habitat transformation and its effects on biodiversity

The human population is increasing, with an annual population growth rate of 2.5% in Africa, the population is predicted to reach 2.5 billion by 2050 (Statistica Research Department 2022), that will lead to an increased demand for food and resources. To meet this demand natural landscapes are increasingly being transformed for agricultural purposes. Globally, land use for commercial agriculture takes up 50% of the Earth’s habitable land with 77% being livestock farming and 23% being crop farming (Ritchie and Roser 2020). In South Africa, agriculture takes up approximately 37% of the land, of which 79% of this land is used for grazing and 21% for crops (Statistics South Africa 2020). Commercial agriculture is one of the main drivers of biodiversity loss in all terrestrial ecosystems found in South Africa, as well as globally (Barger et al. 2018), leading to habitat loss and, in certain cases, extinctions (Benton et al. 2021). In addition to habitat loss, agricultural practices also lead to habitat fragmentation, where large natural areas are being reduced to small, isolated patches (Fahrig 2003), which further exacerbate habitat loss and degradation (Foley 2005). These fragmented landscapes prevent species from moving between or within their niches within their habitat and may leave specialist species vulnerable to competition due to the limited resources (de Lima Filho et al. 2021). Habitat generalists, on the other hand, are not as limited by fragmentation due to their ability to utilize a wide variety of resources from their surroundings (Gentili et al. 2014). The size of the habitat also has an effect on species diversity levels after fragmentation, with large habitats allowing for increased species diversity and smaller habitats reducing the species diversity (Rybicki et al. 2019). Therefore, the effects of fragmentation on biodiversity can either be positive or negative depending on species’ competitive abilities as well as the size of the habitat (Rybicki et al. 2019).

Human-wildlife conflict is another aspect that has a considerable influence on species levels in transformed environments. Firstly, many species that are found in agricultural landscapes are seen as pests, as they alter agricultural production in a negative way, leading to financial losses (Inskip and Zimmerman 2009).). Therefore, farmers might be more tolerant to certain species that do not cause any agricultural damage but try to eradicate species they deem to be pests (Foster et al. 2019). An example is mesopredators, that often reach high densities in anthropogenically transformed environments due to their efficient hunting skills, coupled with their variable prey spectrum (Bagniewska & Kamler 2013). In the

Northwest Province of South Africa black-backed jackal *(Canis mesomelas*) and caracal (*Caracal caracal*) are two of the most killed species because they prey on livestock (Thorn et al. 2012). These two species are also known to prey on a variety of species that utilize burrows for refuge, such as spring hare, and therefore decreased predator numbers might lead to increased numbers of prey species utilizing burrows in these environments. Other species that cause financial losses via crop damage include the Cape ground squirrel (*Xerus inauris*) and the Highveld gerbil (*Gerbilliscus brantsii*) (Foster et al. 2019). Eradication of these species on farms may have an impact on the number of those species using burrows on farms. Another aspect to human-wildlife conflict is the hunting and/or illegal wire snare poaching of species for the bushmeat trade, which has considerable negative impacts on wildlife populations, habitats, and species activity (Watson et al. 2013, Briggs 2017, Martins & Shackleton 2019).

Although agricultural activity may have negative impacts on species, some do benefit, but this is dependent on the species present as well as the type of agricultural activity. Agricultural fields and crop lands provide certain species with more accessible food sources (Carlson 1985). In Argentina, it was found that small mammal habitat generalist species, such as the drylands vesper mouse (*Calomys musculinus),* preferred highly productive agricultural areas, whereas habitat specialist species such as Azara’s grass mouse (*Akodon azarae)* and red hocicudo (*Oxymycterus rufus)* seemed to prefer less productive areas (Gomez et al. 2015). The seasons also have an impact on this. For example, Azara’s grass mouse is more likely to use alternative, more productive crop field habitats when food resources are scarce in its natural habitat (Hodara et al. 2012). Other species benefitting from increased food availability on agricultural land include small generalist rodents, which also frequent burrows for shelter and refuge (Gentili et al. 2014). In addition, the potential increase in the abundance of crop feeding species on farms could lead to an increase in the number of species that prey upon them. For example, in Canada, western burrowing owls (*Athene cunicularia hypugaea*) prefer to nest near irrigated agricultural landscapes due to the increase in prey availability (Moulton et al. 2005). Jackals are another species benefitting from increased prey on farms (Sillero-Zubiri et al. 2004), although, in general, they have been shown to prefer less transformed areas (Ramesh & Dawns 2015). This might be due to farmers having a negative perception of jackals and taking measures to eradicate them (Drouilly et al. 2018).

Given that species’ responses to agriculture vary, both the composition and the diversity of community assemblages living within agricultural landscapes are likely to change along an increasing gradient of agricultural intensification. In addition, many larger species, such as wild ungulates and carnivores, are purposely excluded from farms, which is expected to have knock-on consequences for smaller mammals. Historically, agricultural practices provided a range of wildlife habitat, such as shelter beds, hedgerows, cultivated fields and rotational fields (Moulton et al. 2005). Although these habitats have proved to be useful for foraging, nesting, and refuge, wildlife populations in agriculturally converted landscapes have declined significantly (Carlson 1985, Murphy 2003). Animals that use burrows in these landscapes are no exception and may also be impacted by agricultural activity in different ways.

Small generalist rodents are expected to thrive in agricultural landscapes, due to the increased food sources, causing an increase in species abundance at agricultural sites (Butet et al. 2006, Gentili et al. 2014). This, however, is coupled with a decrease in species diversity since generalist species dominate these environments while specialist species prefer more natural environments (Gentili et al. 2014). Gentili et al. (2014) found that there was no difference in the richness of small rodent species but that differences in diversity were observed with specialist species, both striped field mice (*Apodemus agrarius*) and yellow-necked mice (*A. flavicollis*), were more abundant at natural sites, and generalist species such as wood mice (*A. sylvaticus*) and common voles (*Microtus arvalis*), were more abundant at transformed sites. Agricultural sites favour generalist species possibly due to their ability to be highly mobile and/or their high reproductive rates, thereby outcompeting species that are less mobile and have low reproductive rates (Jennings and Pocock 2009).

In addition, the times that animals are active near burrows, as well as throughout the day, might also differ between natural and transformed environments. In more urbanized environments some species have been known to alter their daily activity times. For example, in urbanised Japan, the wild boar *(Sus scrofa*) has changed its activity time during the hunting season to be more active at night and to hide from hunters during the day (Ohashi 2013). However, information for animals in agricultural settings in southern African settings is limited. An effective way to determine whether vertebrate assemblages and activity times differ between burrows at different sites is to set up camera traps since they are non-invasive and reliable (Rowcliffe et al. 2008).

1.4. Camera trapping as a means to collect data on burrowing mammals

Automated camera traps that are used to monitor and detect wildlife activity are being increasingly used due to their unbiased records of activity (Osborne 2016). Camera traps are a useful resource for conservation and wildlife management since they are non-invasive and leave very little environmental disturbance (Rowcliffe et al. 2008). The analysis of camera trap data is relatively straightforward and easy. Once all false triggers and unwanted images are removed from the dataset, one is left with images that allow for useful information to be extracted manually, or with the help of artificial intelligence programs (Norouzzadeh et al. 2018). In addition, multiple burrows can be monitored simultaneously, allowing for easily increasing sample sizes. Numerous studies have provided insights into burrow use with the help of camera traps. For example, Osborne (2016) added to the lists of of species using aardvark burrows in South Africa (Smithers 1971, Whittington-Jones et al. 2011), bringing the total number of vertebrate species recorded using aardvark burrows in Mapungubwe National Park, Limpopo, South Africa, up to 59 from the initial estimate of 27 species. Furthermore, Netherlands (2020) identified 42 new vertebrate species using, or near aardvark burrows in Gonarezhou National Park, Zimbabwe.

In addition, camera traps help to provide useful information on cryptic, nocturnal burrowing animals such as pangolins (Perera et al. 2022), and other species that are difficult to monitor, such as burrowing seabirds (Bird et al. 2021). Furthermore, in an agricultural context, camera traps have been used to measure various species metrics between different sites. For example, Drouilly and O'Riain (2019), used camera traps to measure species richness, as well as other community diversity indices, such as richness and evenness on small rangelands in the Karoo, South Africa. Although camera traps have proved to be useful in many ecological studies, there are some limitations to their use. Various *in situ* factors such as poor performance in extreme environments, theft, and damage from wildlife sometimes hinder the effectiveness of this method (Newey et al. 2015, Hossain et al. 2016, Meek et al. 2016, Wearn and Glover-Kapfer 2017). Furthermore, although data are obtained without someone being present, there is a limited field of view from the camera, although this is generally sufficient for comparisons.

1.5. Aims and objectives

The aim of this study was to compare the use of aardvark burrows and their immediate surroundings between a protected grassland environment consisting of rangeland for wild ungulates as well as mountainous and rocky areas, and a grassland transformed into crop land and grazing paddocks for domesticated ungulates, by using camera trap monitoring over a period of five weeks. Three objectives were set under this aim: 1. to compare the species richness of the vertebrates using abandoned aardvark burrows in a natural *versus* an agriculturally transformed landscape; 2. to determine whether the encounter frequency, encounter duration and encounter proximity to burrows differed between the two landscapes and 3. to compare species activity times between landscapes.

1.6. Research hypotheses/predictions

It is expected that species that typically benefit from farms are species that benefit from crops. A higher encounter frequency, a proxy for relative abundance, of generalist granivorous species was expected in agriculturally transformed environments due to an increase in food source availability, as well as an increased need for refuge from anthropogenic influences such as trapping and poaching (Carlson 1985, Gentili et al. 2014).

2. Study Area and Study Sites

The study was conducted at two study sites within the Bronkhorstspruit-Middelburg region of South Africa: Telperion Nature Reserve and Zonnebloem farm – a privately owned maize, bean, and cattle farm (Figure 1). The sites fall under the Highveld Grassland Biome of South Africa, with both sites experiencing similar climatic conditions. This region experiences summer rainfall with dry winter periods (Swanepoel 2006). The warmest months are January and February and the coldest is July. Telperion experiences an average daily temperature range of 15.1°C to 26.4°C in summer, and an average daily temperature range of 4.2°C to 18.4°C in winter (Brown et al. 2022). The farm experiences an average daily temperature range of 15°C to 25.1°C in summer, and an average daily temperature range of 4.6°C to 18.9°C in winter (Climate Data 2021). Both sites fall within a region of high priority for conservation, due to the extensive transformation of land by anthropogenic activities (Low and Rebelo 1998). This was evident, since the most prominent activities surrounding these two sites included coal mining, as well as private farming.

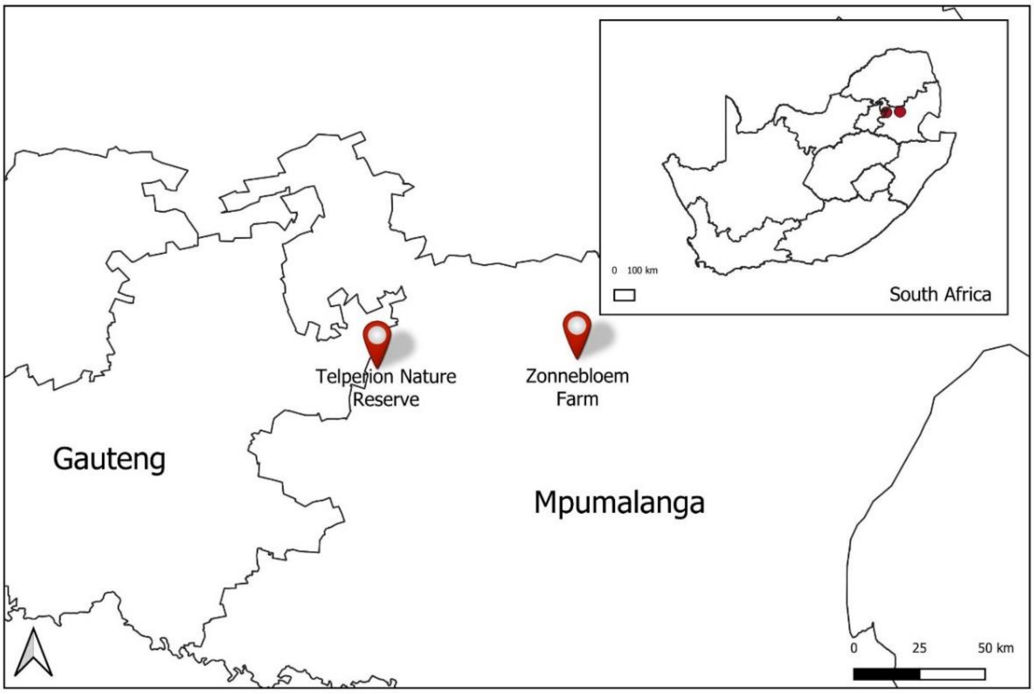

Figure 1: The location of Telperion Nature Reserve and Zonnebloem farm in relation to one another, as well as within South Africa.

2.1. Telperion Nature Reserve

Telperion Nature Reserve, hereafter referred to as Telperion, was where the data for the natural component of the study were collected. Telperion is a privately-owned 7350ha nature reserve located within the Gauteng and Mpumalanga Provinces, approximately 24 kilometres north-east of Bronkhorstspruit, South Africa (25° 40'S and 28° 59'E). Telperion was selected since it was the nearest nature reserve near the farm, still falling within the grassland biome. The reserve borders Ezemvelo Nature Reserve on the east, with the Wilge River forming this boundary.

The vegetation is characterized by Bankenveld vegetation (Figure 2), consisting of Rand Highveld Grassland and Loskop Mountain Bushveld (Mucina and Rutherford 2006). Rocky outcrops, grasslands, and wetlands are prevalent in the reserve, as well as vegetation associated with the Wilge sandstones. Telperion falls within an ecotone between the grasslands of the higher inland plateau and the bushveld of the lower land plateau, and therefore consists of a wide range of plant biodiversity. Telperion historically consisted of old farmlands but has since been transformed into a nature reserve. This region is threatened by mining, agriculture, and development and only two percent of this grassland biome is formally conserved, thus making Telperion an important site for conservation.

Figure 2: An open grassland landscape at Telperion Nature Reserve, showing a camera trap mounted on a pole to the left of the burrow being monitored.

2.2. Zonnebloem farm

Zonnebloem farm, hereafter referred to as the farm, was where the data for the agriculturally transformed landscape component of this study were collected. Zonnebloem is a privately owned 6000-hectare (ha) maize, bean and cattle farm located in Middelburg, South Africa (25° 33'S, and 29° 54'E). The landscape included grazing paddocks for cattle (Figure 3a), maize and bean crops, and small areas of black-wattle (*Acacia mearnsii*) forest (Figure 3b), which separated different sections of the farm. The farm comprises of approximately 65% cropland with the remaining 35% used for cattle farming. Zonnebloem was selected due to it being a large-scale agricultural farm with different agricultural practices of varying intensities. The maize was nearing the end of its growing season and had many maize kernels that could be used for food for animals and was tall enough to provide a sheltered landscape.

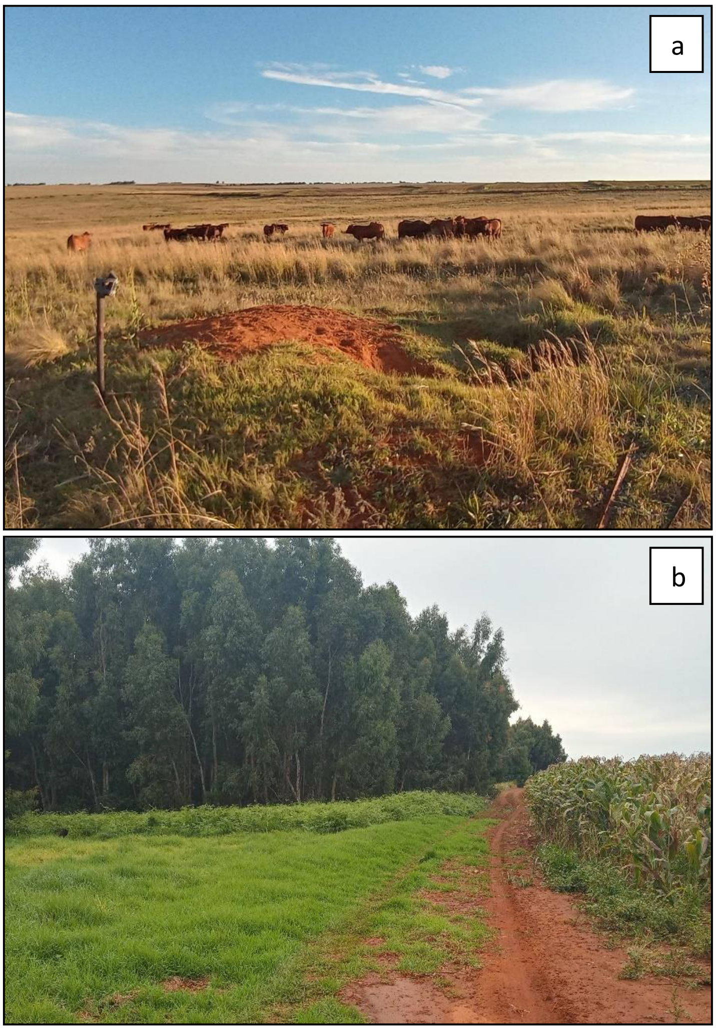

Figure 3: Monitored landscapes at Zonnebloem farm, showing a:) a camera placed in front of a burrow within the open grazing paddocks used for cattle grazing at Zonnebloem farm, and b): small areas of black-wattle (*Acacia mearnsii*) forest (left) and large areas of maize crops (right) to the left and right of the farm's grazing paddocks, respectively.

3. Materials and Methods

3.1. Sampling design and data collection

At both study sites, burrows excavated by aardvark were selected, based on burrow size. Although size is a good indicator of the original burrow creator (Haussmann 2016), some burrows could have been modified by other secondary excavators such as the common porcupine. Only permanent burrows were monitored in this study, i.e. only burrows that extended into the soil and had a tunnel leading into them (Figure 4). In addition, the burrows had to suggest vertebrate occupancy, such as spoor, hair, or droppings nearby as abandoned burrows, identified by the presence of cobwebs across the entrance as well as the presence of long untrampled grass near the bottom of the entrance, would not be suitable for the study.

Figure 4: Examples of burrows at Telperion Nature Reserve and Zonnebloem farm that had tunnels leading into them.

Twenty motion triggered camera traps (Spy-Point Solar Dark, Quebec, Canada) were set up throughout relatively flat, open areas within Telperion, and 17 cameras were set up on the farm in April 2022. The cameras at the farm were set up in open pastoral fields, as well as within the small black-wattle forests near the fields. Transects were walked within each site to locate as many burrows as possible, and any burrows that fit the correct burrow criteria (tunnel leading into burrow, signs of occupancy) were opportunistically selected (Figure 5).

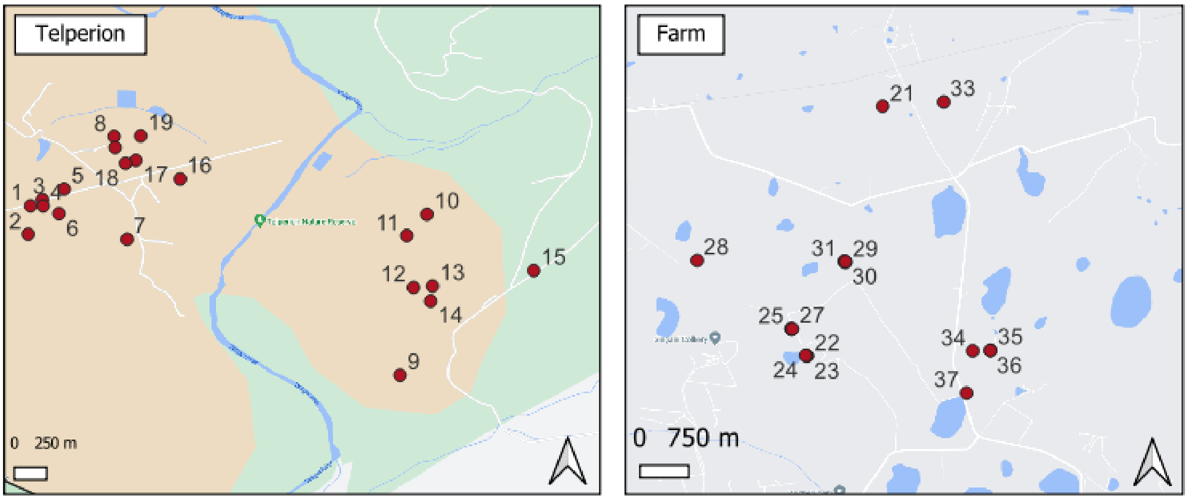

Figure 5: Location of the burrows in relation to each other, within Telperion Nature Reserve and Zonnebloem farm, including each camera's ID number; Telperion (ID 1-20), and the farm (ID 21-37). Some cameras were relatively close to one another and thus appear superimposed on top of one another in the map. Blue areas represent water bodies such as rivers, streams, ponds, and dams; tan and green areas represent nature reserve areas and natural vegetation; grey areas represent farmland.

Cameras were placed approximately 1.5 m from the entrance of each burrow and mounted approximately 70 cm above the ground on a wooden pole that was hammered into the ground. Cameras were secured with cable ties to ensure that they would not move over time and were angled toward the entrance of the burrows to document any animal activity around the burrow (Figure 6). Cameras were placed in a southerly or northerly direction where possible to avoid the glare from the sun during its rising and setting. Any vegetation within a radius of approximately 5 m within the camera's field of view was cleared to prevent any false triggers.

Figure 6: Each camera trap was angled toward the burrow entrance to capture species entering and exiting the burrow, as well as species near the entrance of the burrow and walking past the burrow.

Each camera was programmed to take three photographs when triggered by movement, with ten seconds of inactivity afterwards to reduce the number of images of a single encounter, and to limit vegetation-triggered captures. Each camera was left to record data for approximately five weeks from April to mid-May 2022, with a service and reset occurring at two-week intervals. During this period cameras were checked to see if they had moved or fallen over and were correctly positioned once again. In addition, the data were downloaded, and batteries were tested and replaced. The cameras were then reset to ensure that there would be no overwrite of the data.

3.2. Data processing

Due to cameras being knocked over and other technical reasons, the cameras were not all active for the same amount of time. Therefore, of the 17 cameras that were set up at the farm, only 16 were used, as one of the cameras was knocked down and did not capture anything in the period after the reset. All remaining cameras were operational for at least 5 days, with a range up to 35 days (Appendix). The photographs were sorted, false triggers from moving vegetation were deleted and only those images containing mammals and birds were kept. Other small species of lizards, snakes and invertebrates were not used, as they were too small to identify correctly. For each species, images were then categorized into encounters. To ensure that each encounter recorded was an independent event, a period of 30 min of no sightings of that species was used to separate encounters (O'Brien et al. 2003). For each encounter, the start and end times were recorded, to determine the length and time of each encounter at the burrow.

In addition, for each species, each encounter was categorized based on its proximity to the burrow. Three types of encounters were analysed and were categorized as either "walking past", "investigating" near the entrance, or actually using (exiting/entering) the burrow. Although this process was subjective, there were a number of criteria that were considered when categorizing encounters. Images were assigned to the 'walking past' category when there were generally fewer photos of that species (one to two images), and the species seemingly showed no clear interest in, or had no prolonged interaction with the general burrow area. Encounters were placed in the "investigating" or 'near-entrance' category when the photos showed animals that displayed interest in the general burrow area, typified by a sequence of photos (generally more than two) that showed the animal peering into the burrow (sometimes tentatively) and/or investigating/sniffing around the area. Photos that showed animals lying down, hovering around or being present in the general burrow area for prolonged periods were also placed into this category. Encounters were placed in the 'using' category when a sequence of photos showed a progression of the animal either going into the burrow or exiting the burrow, or both.

Furthermore, since the number of operational days differed between cameras, encounter frequency was standardised to encounters per day, by dividing the total number of encounters by the number of operational camera days. However, given that species richness does not increase linearly with time, as seen with experimental species accumulation curves, it was not sensible to divide the total number of species observed by the number of operational camera days for this variable. Thus, species richness was standardized by using a seven-day rolling average of the daily number of species recorded at each camera. For activity times, only species present at both sites and with more than 5 encounters across both sites were used. The average time was calculated and the percentage of encounters falling into 24 one-hour time intervals was plotted.

3.3. Statistical analyses

Generalized Linear Models (GLMs), Generalized Linear Mixed Models (GLMMs) and Chi-square tests were used within R-Studio version 4.2.1 (RStudio Team, 2022) to test whether there were any differences in the response variables between Telperion and the farm. For species richness and encounter frequency, Poisson distributions were assumed. These response variables were modelled with GLMs, using the glm2 package (Marschner 2011). For these two response variables, cameras were used as replicates (n = 36). For encounter duration a Gaussian distribution was used, following a Shapiro-Wilk test for normality. GLMM models were used, specifically Generalized Linear Mixed-Effects Models (glmer) using the lme4 package (Bates et al. 2015). Cameras were added as a random effect to account for potential differences between cameras, and encounters were used as replicates. The models for encounter frequency and encounter duration were run using only the species present at both sites (13 species) and to measure effect size, Cohen's d was determined when significance differences were found between response variables. Chi-square tests were used to test for associations between burrow proximity and site (Telperion *versus* farm) as well as to test for the association between species presence and site. To ensure that meaningful Chi-tests were performed, only those species that had expected values >5 throughout both Telperion and the farm were used. Fisher exact tests were used to test for association between species presence and site for species with expected values <5. A significance threshold of 0.05 was used throughout. No statistical tests were performed for activity times, as this component was primarily descriptive.

4. Results

4.1. *Species richness*

A total of 47 species were observed between Telperion and the farm, of which 29 were mammals and 18 were birds (Table 1). Hare, lark, pipit and dove species were indistinguishable and, as such, were assigned to each of these broad categories. All rodent species were also grouped into a ‘rodent’ category since they were also indistinguishable. Of the 47 species observed, eight ungulate and one ostrich species were excluded since they cannot reasonably be expected to inhabit intensive agricultural areas, and domesticated cows since they were not present at the Telperion, leaving eight mammal and seven bird species that were disproportionately associated with either site (Table 1). These species were the rusty-spotted genet (*Genetta maculata*), black-backed jackal, yellow mongoose (*Cynictis penicillata*), aardvark, vervet monkey (*Chlorocebus pygerythrus*), honey badger (*Meles meles*), chacma baboon (*Papio ursinus*), Cape porcupine, ant-eating chat, crowned plover (*Vanellus coronatus*), pipit (*Anthus* sp), Cape robin chat (*Cossypha caffra*), tawny flanked prinia (*Prinia subflava*) and masked weaver (*Ploceus velatus*) and dove *sp.* Thirteen species were found at both sites and thus all further statistical analyses were undertaken on these species. Although a number of species were disproportionately associated with either site, overall, there was no statistically significant difference in species richness between the two sites (Z-score = -5.03; *n* = 36; *P* = 0.60).

Table 1: Species composition at Telperion Nature Reserve and Zonnebloem farm, showing the number of camera traps where each species was observed, and the total number of camera traps deployed at each site in parentheses. Species in bold occur at both sites and significant *P*-values from Chi-square (a) and Fisher exact (b) tests show disproportionality of species between sites with a significance level of 0.05*. Species with ‘na’ were not included in the analyses.

	Common name	**Scientific name**	**Telperion (*n*=20)**	**Farm (*n*=16)**	***P*-value**	**Test**
Mammals						
Carnivores	African wild cat	*Felis lybica*	0	3	0.08	b
	Black-backed jackal	***Canis mesomelas***	18	7	< 0.01*	b
	Black-footed cat	*Felis nigripes*	3	0	0.26	b
	Meerkat	*Suricata suricatta*	5	0	0.05	b
	Rusty-spotted genet	***Genetta maculata***	1	10	< 0.01*	b
	Serval	*Leptailurus serval*	0	2	0.19	b
	Slender mongoose	*Galerella sanguinea*	0	3	0.08	b
	Yellow mongoose	***Cynictis penicillata***	15	3	< 0.01*	a
Insectivores	Aardwolf	*Proteles cristata*	1	0	1.00	b
Omnivores	Aardvark	*Orycteropus afer*	13	0	< 0.01*	a
	Chacma baboon	*Papio ursinus*	10	0	< 0.01*	b

	Common name	Scientific name	Telperion (*n*=20)	Farm (*n*=16)	*P*-value	Test
	Honey badger	*Mellivora capensis*	0	11	< 0.01*	b
	Rodent		15	11	0.72	b
	Vervet monkey	*Chlorocebus pygerythrus*	0	5	0.01*	b
Herbivores	[#]Blesbok	*Damaliscus pygargus phillipsi*	11	0	na	na
	Cape porcupine	***Hystrix africaeaustralis***	7	16	< 0.01*	a
	Common duiker	***Sylvicapra grimmia***	1	5	0.07	b
	[#]Common eland	*Taurotragus oryx*	3	0	na	na
	[#]Common zebra	*Equus quagga*	11	0	na	na
	[¥]Domesticated cows	*Bos taurus*	0	4	na	na
	[#]Giraffe	*Giraffa* sp.	2	0	na	na
	[#]Greater kudu	*Tragelaphus strepsiceros*	1	0	na	na
	Hare	***Lepus* sp.**	4	1	0.35	b
	[#]Impala	*Aepyceros melampus*	12	0	na	na
	Spring hare	***Pedetes capensis***	9	2	0.07	b
	[#]Springbok	*Antidorcas marsupialis*	3	0	na	na
	Steenbok	*Raphicerus campestris*	0	1	0.44	b
	Common warthog	***Phacochoerus africanus***	18	11	0.20	b
	[#]Wildebeest	*Connochaetes sp.*	15	0	na	na
Birds						
	Ant-eating chat	***Myrmecocichla formicivora***	19	5	< 0.01*	a
	Cape robin chat	*Cossypha caffra*	0	10	< 0.01*	b
	Common mynah	*Acridotheres tristis*	1	0	1.00	b
	Common stone chat	*Saxicola torquatus*	1	0	1.00	b
	Coqui francolin	*Peliperdix coqui*	3	0	0.24	b
	Crowned plover	*Vanellus coronatus*	7	0	0.01*	b
	Dove	***Columbidae***	1	6	0.03*	b
	Fiscal shrike	*Lanius collaris*	1	0	1.00	b
	Guinea fowl	*Numididae*	2	0	0.50	b
	Kurrichane thrush	*Turdus libonyana*	0	3	0.08	b
	Lark	*Alaudidae*	3	0	0.24	b
	Masked weaver	*Ploceus velatus*	0	7	< 0.01*	b
	[#]Ostrich	*Struthio camelus*	4	0	na	na
	Owl	*Bubo* sp	1	0	1.00	b
	Pipit	***Anthus* sp.**	14	3	< 0.01*	a
	Spotted dikkop	*Burhinus capensis*	1	0	1.00	b
	Swainsons spurfowl	***Pternistis swainsonii***	1	5	0.18	b
	Tawny flanked prinia	*Prinia subflava*	0	4	0.03*	b

[#] Species that are not expected to occur on the farm; [¥] species that are not expected to occur at Telperion; species in bold indicate those species found at both Telperion and the farm

4.2. Encounter frequency

The species with the highest encounter frequency at Telperion was the ant-eating chat (mean ± SD: 1.23 ± 1.23), while the species with the highest encounter frequency at the farm was the Cape porcupine (mean ± SD: 3.05 ± 2.13) (Figure 7; Table 2). Of the 13 species that occurred both at Telperion and the farm, the ant-eating chat, Cape porcupine and ‘rodents’ were the only taxa whose encounter frequencies differed significantly between sites, with the Cape porcupine and rodents observed more frequently at the farm and the ant-eating chat more frequently at Telperion (Table 2). For these species, the Cohen’s d measures were: ant-eating chat = 1.10 (large); Cape porcupine = 1.97 (large); rodent = 0.577 (moderate).

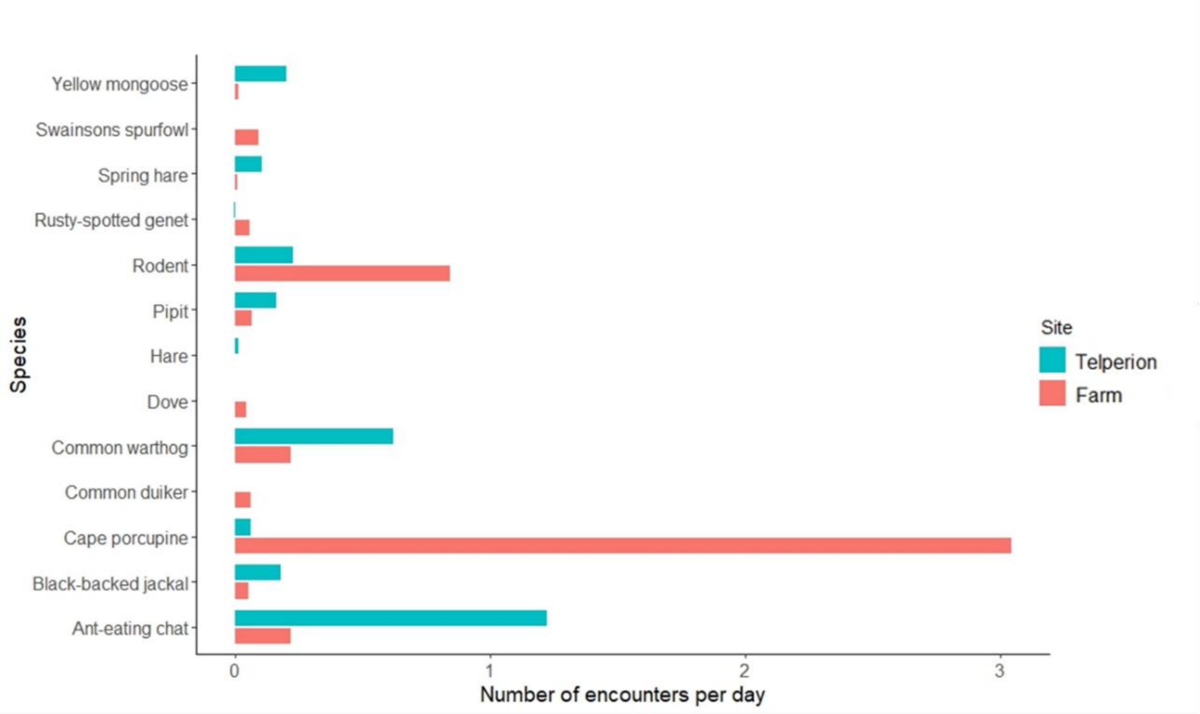

Figure 7: Mean encounter frequency for each species/taxon, showing the total of all three encounter types (walking past, investigating, and entering), occurring at both Telperion and the farm.

Table 2: Generalized Linear Models (GLM) and Generalized Linear Mixed Models (GLMM) results for encounter frequency and encounter duration for total encounters, including sample sizes for 13 species at Telperion (T) and the farm (F). Values for encounter frequency and encounter duration are daily means ± SD.

	Total encounters			Encounter frequency (GLM)			Encounter duration (GLMM)	
Species	T	F	Telperion	Farm	*P*-value	Telperion	Farm	*P*-value
Rusty-spotted genet	2	25	0.00 ± 0.01	0.06 ± 0.05	0.49	1.00 ± 0.00	1.02 ± 0.06	0.78
Black-backed jackal	89	20	0.18 ± 0.18	0.05 ± 0.08	0.31	2.05 ± 2.25	3.76 ± 7.16	0.84
Yellow mongoose	96	4	0.20 ± 0.24	0.02 ± 0.04	0.22	2.21 ± 1.87	1.00 ± 0.00	0.53
Rodent sp.	106	337	0.23 ± 0.25	0.84 ± 1.49	**0.01 (T<F)**	11.32 ± 14.39	9.94 ± 13.75	0.41
Common warthog	287	88	0.62 ± 0.58	0.22 ± 0.27	0.09	5.06 ± 5.60	4.61 ± 7.40	0.35

	Total encounters		Encounter frequency (GLM)			Encounter duration (GLMM)		
Species	T	F	Telperion	Farm	*P*-value	Telperion	Farm	*P*-value
Cape porcupine	33	1268	0.06 ± 0.15	3.04 ± 2.13	< **0.01 (T<F)**	4.62 ± 9.43	11.35 ± 6.99	0.89
Lepus sp.	8	1	0.01 ± 0.03	0.00 ± 0.01	0.75	2.13 ± 1.93	1.00 ± 0.00	0.72
Common duiker	1	30	0.00 ± 0.01	0.06 ± 0.11	0.50	1.00 ± 0.00	1.38 ± 0.84	0.86
Spring hare	53	2	0.10 ± 0.15	0.01 ± 0.04	0.37	4.78 ± 4.69	1.00 ± 0.00	0.54
Dove sp.	1	23	0.00 ± 0.01	0.05 ± 0.07	0.54	1.00 ± 0.00	1.88 ± 0.89	0.58
Swanson’s spurfowl	1	15	0.00 ± 0.01	0.09 ± 0.28	0.44	1.00 ± 0.00	1.40 ± 0.89	0.75
Ant-eating chat	549	42	1.23 ± 1.23	0.22 ± 0.41	< **0.01 (T>F)**	16.04 ± 12.43	7.78 ± 8.34	0.41
Pipit sp.	79	18	0.16 ± 0.19	0.07 ± 0.20	0.43	4.10 ± 4.55	1.69 ± 0.81	0.14

4.3. Encounter duration

For the average encounter duration per species within sites, the ant-eating chat had the longest average duration time in minutes at Telperion (16.04 ± 12.43), and Cape porcupine had the longest at the farm (11.34 ± 7.00) (Figure 8; Table 2). However, no statistically significant differences in encounter duration were found for either of these or any of the other species between Telperion and the farm (Table 2).

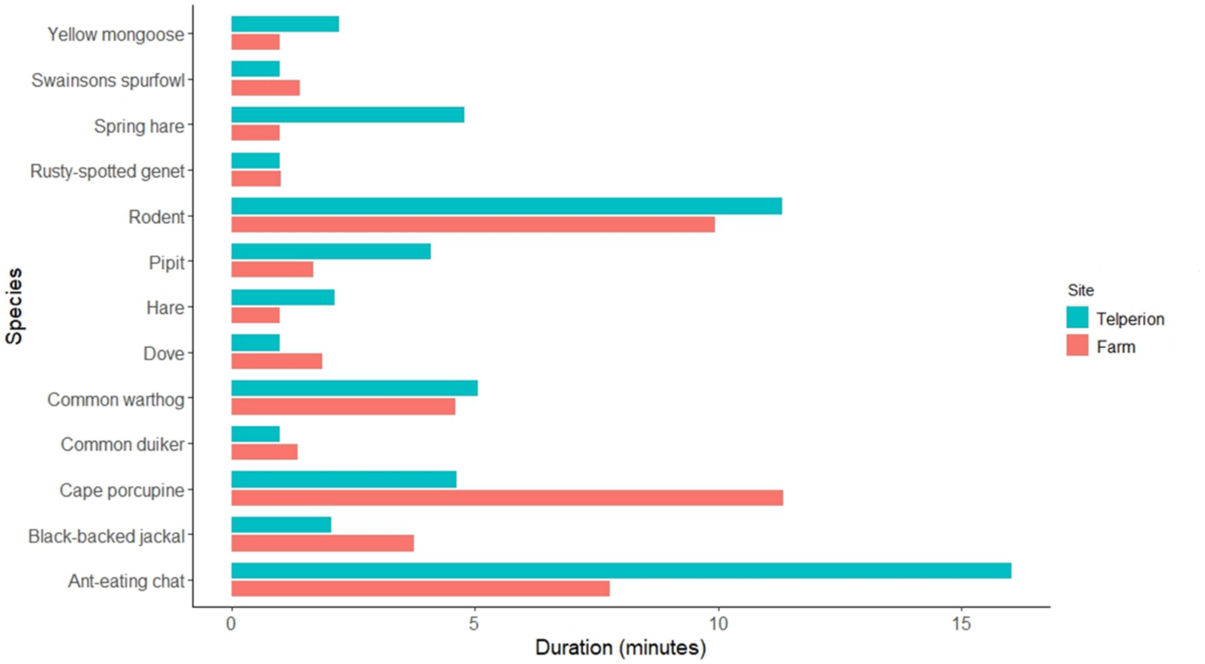

Figure 8: Mean duration of species/taxon encounters at Telperion and the farm in minutes. Species active for one minute or less were grouped into the 1-minute category.

4.4. Burrow proximity

Of the six species/groupings that had greater than five encounters throughout both Telperion and the farm, only four species showed statistically significant differences in burrow proximity between sites, namely black-backed jackal, common warthog, 'rodent', and ant-eating chat (Table 3). Black-backed jackals were more often near the entrance of the burrows at the farm compared to just walking past the burrows at Telperion. Cape porcupines and 'rodents' entered or exited the burrow more frequently at the farm, whereas the common warthog entered or exited the burrows more at Telperion (Figure 9).

Table 3: Chi-square test results for burrow proximity for the species for which the expected values were greater than five throughout the observation period at both Telperion (T) and the farm (F), with a statistically significance threshold of 0.05 and degree of freedom = 2. Three proximity categories (walking past, near entrance, entering/exiting) are depicted and scored, based on the percentage of encounters, as greater than, smaller than or equal at both sites.

Species	Chi-square	p	Proximity
Rodent sp.	62.46	**< 0.01**	Walking past: T = F; Near entrance: T > F; Entering/exiting: T < F
Common warthog	27.89	**< 0.01**	Walking past: T < F; Near entrance: T < F; Entering/exiting: T > F
Cape porcupine	5.31	0.07	All proximities: T = F
Ant-eating chat	6.57	**0.04**	Walking past: T > F; Near entrance: T < F; Entering/exiting: T > F

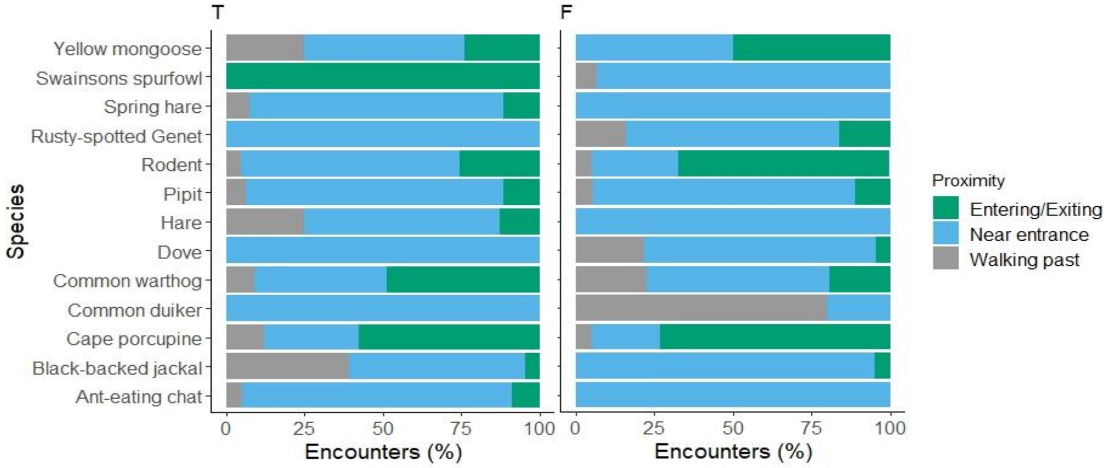

Figure 9: Distribution of species encounters between the three burrow proximities at Telperion (T) and the farm (F) and the relative proportion of entering/exiting the burrow (green), near the entrance of the burrow (blue), and walking past the burrow (grey).

4.5. Activity times

There were no visible differences between species' activity times between the sites (Figure 10). Both bird species, namely ant-eating chat and pipit sp. were mostly diurnal along with warthog, whereas jackal, porcupine and the rodents were mostly either crepuscular or nocturnal.

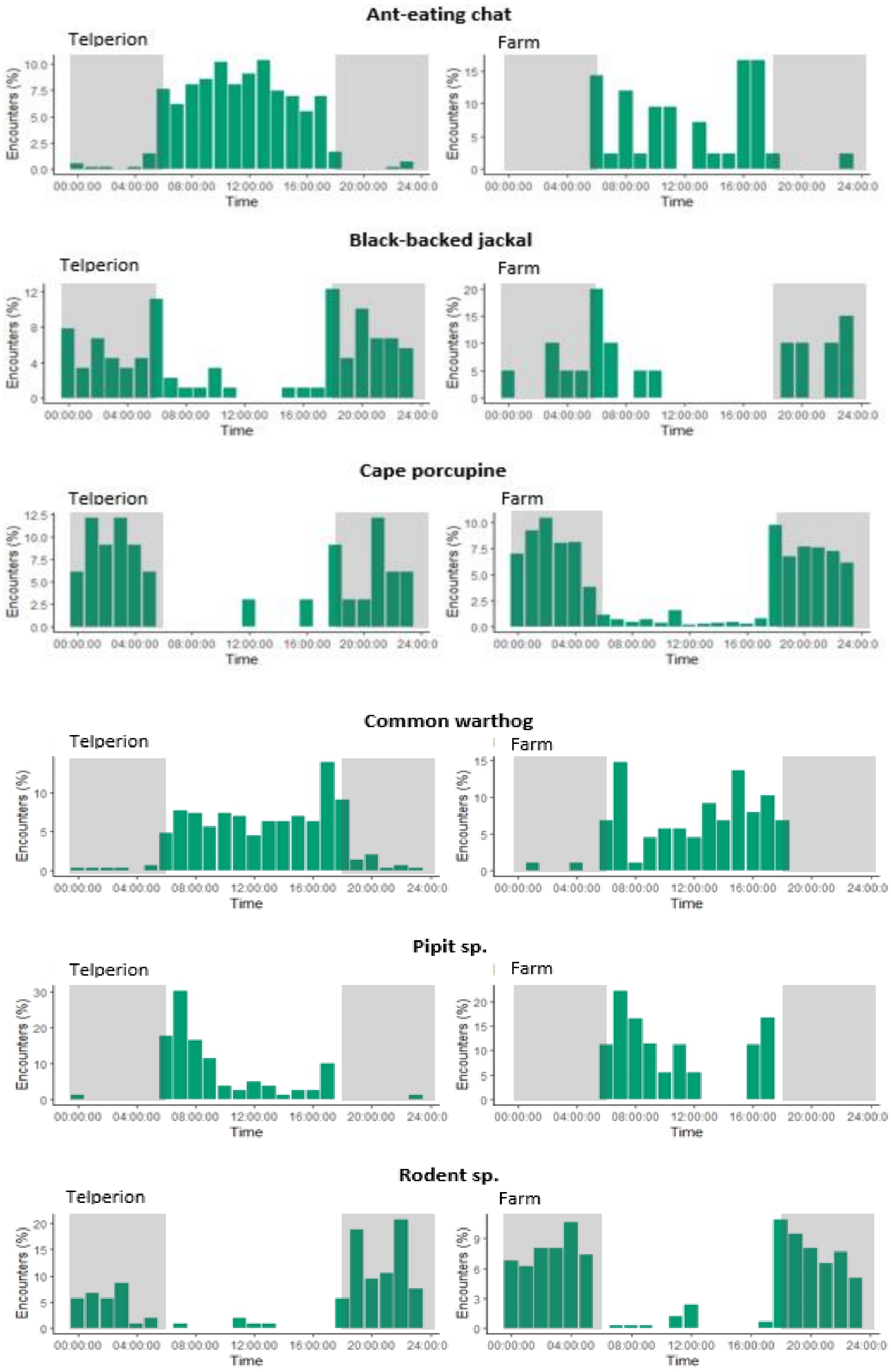

Figure 10: Activity times for species at Telperion and the farm. Only species with more than five encounters across both sites are shown.

5. Discussion

Burrows provide shelter to a wide range of species in South Africa, with 59 species being recorded in a previous study (Osborne 2016). In this study, 37 species were recorded, and only 13 of these species were found at both Telperion and the farm. Species richness between sites did not differ significantly, however, there were different species present at each site. Previous studies suggest that carnivorous mammals are typically associated with less transformed sites, likely due to increased human-wildlife conflict on farms (Thorn et al. 2012), while granivorous rodents, such as Cape ground squirrels and Cape porcupine (Mulungu 2017), but also guinea fowl (Prinsloo et al. 2008), and African wildcats (Skinner and Chimimba 2005) are attracted to transformed farm areas, since they are able to utilize maize fields and grazing paddocks to their advantage or prey on the species that do so. Although the results presented here do not completely concur with these studies in terms of the exact differences in species between the two site types, they do confirm that agricultural settings host different species assemblages to protected areas.

This study assessed both the number of burrows where a species was encountered, as well as the number of times that a species was encountered. Whereas the former gives an idea of how widespread a species was at each site (spatial frequency), the latter can be considered as a measure of how often the species occurred (temporal frequency). Both of these can be considered as proxies for relative abundance. Of the 37 species found in this study, seven species were disproportionately associated with the Telperion burrows (i.e. they occurred at more burrows than expected based on an even distribution). For example, black-backed jackal and spring hare were observed at fewer than half of the farm burrows, but at the majority of the Telperion burrows, suggesting that their population sizes have been reduced substantially at the farm. In addition, four of these seven species were unique to Telperion, i.e. they were not observed at any of the farm burrows. Of these, the aardvark and baboon stand out, as they were observed at more than half of the Telperion burrows, but none of the farm burrows, suggesting drastically reduced numbers of these species at the farm. Some of these species that occurred at fewer burrows than expected at the farm, were also observed less frequently at the farm. More specifically, the ant-eating chat was observed, on average, almost six times less often at the farm than at Telperion. Species that showed significant differences is encounter frequency between sites, namely Cape porcupine, ant-eating chat, and rodent species also had significant effect sizes.

For some of these species, their reduced abundance – and for some possibly even absence – at the farm could be attributable to hunting, or relicts of previous hunting (Coetzee 1979, Thorn et al. 2012, Drouilly et al. 2018, Stuart & Stuart 2019), as well as trapping (Schurch et al. 2021), as a form of lethal control of species considered to be agricultural pests. For example, according to the farmer, jackals were hunted on the farm in previous years, although not as much recently. Hunting could explain the lower abundance of jackals, but also potentially baboons (Drouilly et al. 2018) at the farm. Similarly, whilst Minnie et al. (2016) reported that species commonly found in traps in agricultural settings included aardvark, aardwolf, bat-eared fox, duiker, small spotted genet, small grey mongoose, water mongoose, yellow mongoose, striped polecat, scrub hare, African wild cat, and ground squirrel, this could explain why certain species, such as the aardvark and meerkat were not found at the farm. Another potential reason for the reduced abundance of some species, which is similar to trapping, is illegal wire-snare poaching for bushmeat. During the study this was witnessed at four of the burrows at the farm, and the farmer confirmed that it was a problem at the farm site. Wire-snare poaching for either the bushmeat trade or for subsistence poaching is increasing and has exacerbated conservation problems due to the declines in wildlife populations, as well as receding wildlife habitats (Watson et al. 2013, Briggs 2017, Martins & Shackleton 2019), yet few studies have assessed wire-snare poaching in South African agricultural areas (Kendon 2021). Many species are typically poached for bushmeat in South Africa, including common duiker (*Sylvicapra grimmia*), blue duiker (*Philantomba monticola*), bushbuck (*Tragelaphus scriptus*), scrub hare (*Lepus saxatilis*), bushpig (*Potamochoerus pocus*), vervet monkey (*Cercopithecus aethiops*), large grey mongoose (*Herpestes ichneumon*), water mongoose (*Atilax paludinosus*) and large spotted genet, however, wire-snare poaching is indiscriminate and hunters have been shown to take anything they come across (White 2004).

Habitat suitability is another factor contributing to species abundance, with terrain characteristics as well as resource availability playing key roles. The landscape at Telperion varies, in that there are large, open areas of continuous grassland, as well as areas with dense trees and shrubs, and rocky outcrops and more rugged, hilly areas. On the other hand, much of the landscape at the farm had been transformed into crop land and grazing paddocks, the latter of which were small, isolated patches of grassland in between the crops and small black-wattle forest patches. For example, bird species such as ant-eating chats, various pipit species and crowned plovers are often found within open grassland environments (Lipsey et al. 2015, Wiersma et al. 2020, eBird 2022), with high grass densities (Maphisa et al. 2017), which could explain why these species were found at a higher proportion of burrows at Telperion than at the farm. In addition, although chacma baboons are known to survive in a variety of habitats, often near human activity (Chowdhury et al. 2020) and are able to exploit resources for survival when needed (Barton et al. 1992), they are more common in areas with rugged terrain (Whiten et al. 1987; Drouilly et al. 2018). The lack of mountainous regions at the farm could also explain their absence. Furthermore, the lack of availability of a specialist species' food resource at the farm could explain why there were few to no sightings of these species at the farm; aardvark being a notable example. Aardvark were observed frequently at Telperion and yet aardvark burrows were present at the farm and aardvark would be expected to be there, (Foster et al. 2019, Blomsterberg Reyneke 2022), their lack of presence was alarming. This could potentially be due to the small number of termite mounds at the farm, as termites form a large part of their diet (Melton 1976).

Conversely, some species were more abundant at the farm, with eight species being disproportionately associated with the farm burrows. For example, rusty-spotted genet and Cape porcupine were observed at fewer than half of the Telperion burrows, but at the majority of the farm burrows, suggesting that their populations sizes have increased substantially at the farm. In addition, five of these eight species were unique to the farm, of which the honey badger and vervet monkey stand out since one would expect them to have also been present at Telperion. Some of these species that occurred at more burrows at the farm, were also observed more frequently. For example, Cape porcupine were observed significantly more times each day at the farm than at Telperion. Similarly, rodents were also observed more frequently at the farm, although there was no significant difference in the number of burrows that they were found at between the two sites. The increased abundance of some of these species at the farm could possibly be attributed to the farm providing a more suitable habitat, regarding resource availability, competition between species, and differences in terrain characteristics.

Many generalist species might benefit from the increased food resources found at the farm, allowing their populations to thrive. For example, granivorous rodents, including the Cape porcupine, benefit from the increased maize and food storage opportunities provided by the farm (Reichman & Fay 1983, Skinner and Chimimba 2005, Foster et al. 2019) and therefore their increased presence at farm burrows was expected. Many of the burrows with adult porcupines also had juveniles, suggesting that their populations are thriving within the farm's agricultural environment. Furthermore, porcupines have been shown to prefer ripe maize usually present in the summer months of the year (Hodara et al. 2000), yet this study was undertaken over the autumn months of April and May in South Africa. This might show that porcupine encounters are independent of season and will occur throughout the year depending on whether maize is cultivated yearly or seasonally. However, a study conducted over a longer period of time that incorporates all the seasons will provide useful information on seasonality. This result allows us to accept our hypothesis of expecting a higher encounter frequency of generalist granivorous species occurring in an agricultural site due to the increased food availability. Smaller rodents, such as mice and rats, generally found on agricultural fields are typically generalist species (Gentili et al. 2014), however, limitations due to the quality of the camera trap photographs did not enable the present study to identify these rodents to species level and as such cannot confirm whether they were generalist or specialist species. Small mammal traps at each burrow, coupled with camera trap footage would be useful in future studies. Other generalist species such as rusty-spotted genets, honey badgers, and vervet monkeys are opportunistic in their dietary preferences, enabling them to be highly adaptable in changing environments, and thus likely preferred the farm over Telperion (Wrangham 1981, Robert et al. 2007, Beasley et al. 2011, Widdows 2015). Therefore, the increased food resources which are easily accessible at the farm, over the possible decreased and more dispersed food resources at Telperion, provide increased benefits to some species at the farm.

The increased abundance of species at the farm can also be attributed to other aspects of habitat suitability, such as differences in terrain and tree/canopy cover, as well as competition. Much like black-backed jackals, rusty-spotted genets and honey badgers are also mesopredators, whereby competition influences habitat use. The lack of large predators at the farm could have allowed for the increase in rusty-spotted genet and honey badger abundance, due to decreased competition between the large predators and the mesopredators. Kheswa et al. (2018) investigated how predator assemblages affect honey badger presence in iSimangaliso Wetland Park, South Africa, and found that the presence of leopards (*Panthera pardus pardus*) negatively affected honey badger abundance, while the presence of spotted hyaena (*Crocuta Crocuta*) had a positive influence. Leopards are known to be present at Telperion, which could explain the absence of honey badgers, yet hyaenas are also present. Furthermore, Kheswa et al. (2018) also noted a higher occurrence of honey badger presence in *Eucalyptus* plantations compared to the natural area, which could explain the increased abundance of honey badgers within the black wattle forests at the farm, suggesting that plantation-like landscapes might be preferable. In addition, vervet monkeys which are found in natural areas near water sources and within tree canopies (Wrangham 1981), might also not have been observed at Telperion due to the lack of tree canopy which was abundant in the majority of burrow locations at the farm. Therefore, diet preference, competition between species, and terrain characteristics all influence species in different ways, with the farm environment being more preferable for generalist and opportunistic species, as well as for species that thrive in areas with increased tree canopy cover.

In this study, few species showed statistically significant differences in their proximity to the burrows. Similarly, the duration of activity (i.e. how long the species spends at the burrows) as well as the times that animals were active (i.e. diurnal, or nocturnal) did not differ significantly between sites, despite the spatial and temporal differences in encounter frequencies. This suggests that time spent by species at burrows, the type of activity being conducted, as well as the time of day that they are active at the burrows are not affected by agricultural landscapes. Nocturnal species such as black-backed jackals, Cape porcupines and rodents, displayed nightly activity and diurnal species such as ant-eating chat, common warthog, and pipit species, displayed daily activity as expected (Skinner & Chimimba 2005). Unlike urban environments, agriculture does not really cause a change in the timing of light conditions or human-activity times, which might cause diurnal and nocturnal changes in activity within urban environments (Gaston et al. 2017, Sanders et al. 2021). The lack of a change in animal activity times in this study is therefore not unexpected.

6. Conclusion

This study showed that a variety of species use aardvark burrows within an agricultural environment in the grassland biome, thus highlighting the potential role that agricultural areas that incorporate grazing paddocks and crop land might play in the conservation of wild species. When compared to the natural site, different assemblages of species were found utilizing aardvark burrows at the agricultural site. Some species are favoured by agricultural environments such as rusty-spotted genets, Cape porcupine, honey badgers, vervet monkeys and rodents, due to possible increased resources, whereas other species such as ant-eating chats, aardvark, black-backed jackal, spring hare, and baboons, are not because of a possible relict of past hunting or trapping of animals that were considered agricultural pests in combination with current poaching for bushmeat, as well as habitat unsuitability. This suggests us that although agricultural areas still provide the necessary shelter and foraging opportunities for some species, it is not the case for all, with some species being more tolerant of transformed environments, while others are extremely sensitive. Furthermore, agricultural landscapes do not necessarily alter the ecology of species, and thus the support of wildlife currently using agricultural landscapes for resources and survival would be beneficial for the prolonged survival of those species, especially regarding any threatened or endangered species as well as keystone species such as the aardvark.

Protected areas need to remain protected and cannot be replaced by agricultural spaces, however, agricultural spaces have the potential to become more wildlife-friendly and contribute to conservation. Specifically, a shift in negative perceptions by farmers towards certain mesopredators and implementation of methods that facilitate the coexistence of both livestock and/or crops and wildlife would benefit conservation (Whitehouse-Tedd et al. 2021). In addition, the relationship between bushmeat hunting and food security is complex (Hopcraft et al. 2015) and should be addressed for the benefit of rural communities, wildlife, and farmers. Therefore, research targeted at the bushmeat trade in South Africa is crucial to enable governments and stakeholders to implement efficient conservation strategies. In agricultural areas found within grasslands, a balance needs to be found between agricultural production and the conservation of species found within those areas.

The co-existence of nature conservation and agricultural production should be improved in this region, but would require comprehensive policy coordination, complex spatial planning, and a change in perceptions in support of agricultural communities as well as conservationists, to ensure sustainable land use management in the future (Farkas & Kovács 2021). The results from this study provide a better understanding of the extent to which different organisms use burrows in agricultural environments and will aid in conservation efforts in the future within areas impacted by rapidly expanding agricultural landscapes. The results obtained from this study can be a useful tool when determining how the greater landscape is affected by agricultural activity, and a comparative analysis from other sites within this region would prove to be beneficial. Samples sizes need to be large enough and issues such as pseudoreplication and spatial autocorrelation need to be accounted for. Future research should continue to analyse the factors that influence burrow dwelling animal activity to ensure that adequate conservation strategies can be implemented if required. It is also recommended that a combination of sampling methods be used (Zak & Riley 2016), such as camera traps, surveys or questionnaires, and small animal traps to address any mismatches in the acquired data.

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Appendix: Table showing the location and ID number of cameras at both Telperion (T) and the farm (F), as well as the dates and times of installation, reset and removal of cameras. Total days out = the total amount of days each camera was out in the field; Total working days out = the total number of days that each camera had taken reliable images to use in analyses before reset and removal.

Site	No.	ID	Latitude	Longitude	Camera installed	Last reliable image before reset	Reset	Last reliable image before removal	Removed	Total days out	Total working days out
T	1	N47	-25.713020022958517	28.965386962518096	7/04/2022 12:30	22/04/2022 11:50	22/04/2022 11:50	12/05/2022 15:10	12/05/2022 15:10	35	35
T	2	N8	-25.715203005820513	28.96520096808672	7/04/2022 13:30	22/04/2022 10:30	22/04/2022 13:00	12/05/2022 14:40	12/05/2022 14:40	35	35
T	3	N36	-25.712540997192264	28.966297991573811	7/04/2022 14:00	22/04/2022 13:50	22/04/2022 13:50	03/05/2022 21:16	12/05/2022 15:30	35	26
T	4	N28/N33	-25.713025974109769	28.966358006000519	7/04/2022 15:00	22/04/2022 14:30	22/04/2022 14:30	28/04/2022 14:34	12/05/2022 16:00	35	21
T	5	N34	-25.711722001433372	28.967970013618469	7/04/2022 16:00	22/04/2022 16:50	22/04/2022 16:50	13/05/2022 08:17	13/05/2022 09:00	36	30
T	6	N17	-25.713622011244297	28.967574974521995	8/04/2022 09:00	22/04/2022 16:24	22/04/2022 16:30	25/04/2022 01:00	13/05/2022 08:50	35	17
T	7	N27	-25.715599972754717	28.972817016765475	8/04/2022 09:20	17/04/2022 08:33	23/04/2022 09:20	30/04/2022 10:20	13/05/2022 12:00	35	16
T	8	N45	-25.707671027630568	28.971814038231969	8/04/2022 10:00	23/04/2022 10:31	23/04/2022 10:40	01/05/2022 00:52	13/05/2022 10:30	35	23
T	9	N39	-25.726064024493098	28.993831034749746	8/04/2022 16:20	24/04/2022 14:49	24/04/2022 14:50	04/05/2022 07:05	14/05/2022 10:40	36	26
T	10	N3	-25.713682025671005	28.995905974879861	09/04/2022 10:50	24/04/2022 10:04	24/04/2022 12:40	10/05/2022 21:46	14/05/2022 13:20	35	31
T	11	N29	-25.715310964733362	28.994344007223845	09/04/2022 11:20	24/04/2022 12:05	24/04/2022 13:30	26/04/2022 12:14	14/05/2022 14:00	35	17
T	12	N26	-25.719311982393265	28.994861003011465	09/04/2022 12:00	24/04/2022 13:50	24/04/2022 13:50	10/05/2022 09:09	14/05/2022 11:10	35	31
T	13	N30/N46	-25.719201005995274	28.996328003704548	09/04/2022 13:00	11/04/2022 11:07	24/04/2022 14:10	14/05/2022 09:19	14/05/2022 09:20	35	22
T	14	N40	-25.720360977575183	28.9961819909513	09/04/2022 14:10	24/04/2022 09:31	24/04/2022 14:30	14/05/2022 09:30	14/05/2022 09:30	35	35
T	15	N23	-25.718005998060107	29.004118982702494	09/04/2022 15:00	24/04/2022 15:06	24/04/2022 15:30	01/05/2022 07:30	14/05/2022 10:00	35	23
T	16	N32	-25.710948016494513	28.976911995559931	10/04/2022 08:20	18/04/2022 12:15	24/04/2022 08:40	08/05/2022 11:38	13/05/2022 09:20	33	24
T	17	N20	-25.709510017186403	28.973485976457596	10/04/2022 09:00	12/04/2022 17:52	23/04/2022 11:20	27/05/2022 11:05	13/05/2022 10:10	34	8
T	18	N46/N28	-25.709738004952669	28.972701011225581	10/04/2022 10:30	11/04/2022 14:05	23/04/2022 12:50	06/05/2022 14:43	13/05/2022 11:30	34	27
T	19	N16/N14	-25.707630040124059	28.973866011947393	10/04/2022 11:00	17/04/2022 20:32	23/04/2022 14:40	26/04/2022 06:14	13/05/2022 11:10	34	12
T	20	N49	-25.708521036431193	28.971898024901748	10/04/2022 11:30	23/04/2022 10:54	23/04/2022 15:30	03/05/2022 10:19	13/05/2022 10:30	34	24
F	21	N37	-25.643450981006026	29.75596597418189	13/04/2022 15:10	26/04/2022 09:30	26/04/2022 09:30	30/04/2022 20:47	15/05/2022 13:20	32	17
F	22	N7	-25.681824004277587	29.744384028017521	14/04/2022 09:20	25/04/2022 16:51	26/04/2022 11:00	04/05/2022 03:08	16/05/2022 11:40	32	21

F	23	N44	-25.681902961805463	29.744332982227206	14/04/2022 09:40	25/04/2022 16:41	26/04/2022 11:10	02/05/2022 00:25	16/05/2022 11:50	32	19
F	24	N2	-25.681764995679259	29.744127038866282	14/04/2022 10:00	26/04/2022 11:20	26/04/2022 11:20	16/05/2022 11:30	16/05/2022 11:30	32	32
F	25	N21	-25.677661970257759	29.741884963586926	14/04/2022 11:30	26/04/2022 12:20	26/04/2022 12:20	16/05/2022 12:30	16/05/2022 12:30	32	33
F	26	N48	-25.677773030474782	29.741989988833666	14/04/2022 12:00	26/04/2022 12:10	26/04/2022 12:10	16/05/2022 12:20	16/05/2022 12:20	32	32
F	27	N42	-25.677700024098158	29.742095014080405	14/04/2022 12:30	14/04/2022 18:16	26/04/2022 12:30	09/05/2022 15:16	16/05/2022 12:10	32	15
F	28	N4	-25.667159026488662	29.727444034069777	14/04/2022 12:50	26/04/2022 13:37	26/04/2022 13:40	15/05/2022 15:46	15/05/2022 15:50	31	32
F	29	N50	-25.667475024238229	29.750245995819569	14/04/2022 14:00	25/04/2022 13:20	25/04/2022 13:20	04/05/2022 09:30	15/05/2022 15:10	33	21
F	30	N1	-25.66734803840518	29.750148011371493	14/04/2022 14:20	22/04/2022 05:53	25/04/2022 12:50	09/05/2022 15:44	15/05/2022 15:20	33	24
F	31	N24	-25.667275032028556	29.750051032751799	14/04/2022 14:30	25/04/2022 13:00	25/04/2022 13:00	15/05/2022 15:25	15/05/2022 15:25	33	33
F	32	N31	-25.667319037020206	29.750267034396529	14/04/2022 14:50	25/04/2022 12:40	25/04/2022 12:40	09/05/2022 13:22	15/05/2022 15:30	33	27
F	33	N11	-25.642787972465158	29.765372984111309	14/04/2022 15:50	26/04/2022 01:38	26/04/2022 09:00	27/04/2022 08:38	15/05/2022 12:50	31	14
F	34	N22	-25.68107801489532	29.769825031980872	14/04/2022 16:45	15/04/2022 12:00	25/04/2022 13:00	01/05/2022 15:56	15/05/2022 12:50	31	6
F	35	N10	-25.681008026003838	29.772558035328984	15/04/2022 11:10	17/04/2022 16:04	25/04/2022 14:40	01/05/2022 07:38	15/05/2022 14:50	30	10
F	36	N43	-25.681040966883302	29.772526016458869	15/04/2022 11:20	20/04/2022 01:59	25/04/2022 15:00	na	na		
F	37	N15	-25.687577007338405	29.768879972398281	15/04/2022 11:30	19/04/2022 12:50	26/04/2022 12:42	02/05/2022 10:20	15/05/2022 14:00	30	12