

Proximity to Humans Reduces Distance to Foraging Sites by Aardvarks

Nolutho Makwati¹, Zivanai Tsvuura^{1,2}, and Manqhai Kraai^{3,*}

¹Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, 3209, South Africa.
E-mail: luluthomakwati@gmail.com (Makwati)

²Department of Biodiversity, School of Molecular and Life Sciences, Faculty of Science and Agriculture, University of Limpopo, Sovenga, 0727, South Africa. E-mail: zivanai.tsvuura@ul.ac.za (Tsvuura)

³Faculty of Applied and Natural Sciences, Sol Plaatje University, Private Bag X5008, Kimberley, 8300, South Africa.

*Correspondence: E-mail: Manqhai.Kraai@spu.ac.za (Kraai)

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Aardvarks change the ecosystem through digging for food and shelter thus providing habitats for various animals in sub-Saharan Africa. We determined use of the landscape and foraging behaviour of aardvarks in a communal area. We aged and quantified aardvark foraging burrows and dens in the dry, wet and early dry seasons of 2020 and 2021 in Ncunjane village of KwaZulu-Natal Province, South Africa. We used 50 m × 10 m belt transects to quantify aardvark foraging burrows in each site of aardvark activity. For each aardvark foraging burrow, we determined age and measured the maximum depth and two perpendicular lengths on the ground surface. We recorded numbers of active dens, active and inactive entrances for each den, distances between active entrances of a den and size of the den. We recorded any animal activity or trace (e.g., animal faeces and spider webs) on the den entrances. Aardvarks dug shallow and deep foraging burrows in the wet and dry seasons, respectively. All seasons comprised a greater number (> 51%) of old than new and very old foraging burrows. Aardvarks showed human avoidance by restricting their foraging activities to the rangeland rather than within the village. Dens were constructed close (within 50 m) to feeding areas, which may be necessary in a human-dominated environment. Villagers closed den entrances closer to homes with rocks to prevent snake habitation and used the den entrances as dumping sites for rubbish and disposable nappies. Ultimately, aardvarks appeared to regulate their behaviour by keeping their activities in the outskirts of the village, feeding closer to dens, creating many entrances for escape and thus limited space utilised compared to their counterparts in protected areas. Human activities will likely drive aardvarks away or facilitate local extinction. The study encourages active conservation efforts in marginalised communal areas.

Keywords: Communal area, Dens, Foraging burrows, Human activity, Rangeland

BACKGROUND

Animal behaviour has been studied extensively and shows that animals alter their behaviour for food and predation (Owen-Smith 1994; McArthur et al. 2014). Seasonality also influences animal behaviour. For example, in the wet season when food is readily available, predators may use vegetation to be inconspicuous and surprise their prey. As such, prey may feed

in more open areas to avoid predators or at least see them coming (Valeix et al. 2009). Living with people or close to them introduces another dimension to animal behaviour and behavioural adjustments thereof. Wildlife and its proximity to people tends to result in human-wildlife conflict (HWC), where animals may be hurt or killed if they encounter people (Nyhus 2016). Animals may then learn to shape their behaviour to avoid and/or evade human contact. The role of HWC has been studied

for large-sized and ‘dangerous’ animals such as leopards (*Panthera pardus*), lions (*Panthera leo*), elephants (*Loxodonta africana*) and crocodiles (*Crocodylus nilotica*), among others (Marowa et al. 2021; Burak et al. 2023). In these instances, one of the parties may be hurt or killed. However, there are less harmful animals like the armadillo (*Oryzomys afer*), which suffer from hunting pressure regardless (Makwati et al. 2023).

Hunting may induce a change in animal behaviour. For example, the European red deer, *Cervus elaphus*, sought a more inconspicuous habitat during the hunting season (Lone et al. 2015). The animals chose survival over sites with bilberry (*Vaccinium myrtillus*), an important plant to their diet. Other animals like the wild boar (*Sus scrofa*) may change from diurnal to nocturnal activity to minimise contact with people (Keuling et al. 2008). In addition, wild boar may increase or decrease their home range where hunting took place (Calenge et al. 2002; Keuling et al. 2008). Humans can thus influence the foraging behaviour and landscape utilisation of wild animals via hunting activities (Lodberg-Holm et al. 2019).

Armadillos create elaborate diggings for food and shelter in the landscapes in which they occur (Taylor and Skinner 2004). In so doing, the animal creates microhabitats that can be utilised by other species such as the Karoo toad *Bufo garrispensis*, the ground agama *Agama aculeata* and Cape porcupine *Hystrix africaeaustralis*, which use the burrows for shelter, thermoregulation and moisture (Whittington-Jones et al. 2011). Compared to other burrowing animals, armadillo diggings are abundant and deep (Taylor and Skinner 2004; Kingdon et al. 2013), which makes armadillos one of the most effective ecosystem engineers (Haussmann et al. 2018).

A den is a burrow system that incorporates a network of several burrows (Hagenah et al. 2013). For armadillos, the den can comprise up to eight different entrances connected by short lateral tunnels (Kingdon et al. 2013). Armadillos use these multiple entrances to enter and leave for feeding (Melton 1976; Taylor and Skinner 2004). The dens are large to accommodate the large body size (40–80 kg) of the animal. Armadillos may also use abandoned dens within their home range instead of digging new burrows (Taylor et al. 2002). The burrows dug by ecosystem engineers vary in size and depth because of the physical properties of soil (Reichman and Smith 1990), e.g., soil with fewer rocks is easy to dig (Shenbrot et al. 1997).

Armadillo digging activities may be influenced by prey availability and seasonality (Lindsey et al. 2013). Armadillos feed on termites dominantly in the wet season and on ants during the dry season (Taylor et al. 2002; Kingdon et al. 2013). The extent (burrow

number and size) of digging foraging burrows depends on food availability (van Aarde et al. 1992; Taylor and Skinner 2003). Ants and termites are small invertebrates which are consumed by armadillos in large quantities to meet their energetic requirements (Kingdon et al. 2013). The feeding requirements of armadillos result in the abundance of their foraging activities, i.e., foraging burrows and destruction of termite mounds in the landscape, while dens occur to a lesser extent. The size (depth) of the foraging burrows is influenced by prey type, for armadillos dig deeper to catch termites compared to ants (Taylor et al. 2002). Armadillos also dig to create escape routes underground (temporary burrows) from predation or other threats. Such burrow systems may increase the abundance of dens in the landscape. Burrow networks facilitate escape and would likely increase in human-dominated ecosystems. People with livestock tend to keep dogs for the safeguarding of their homesteads (Van Sittert and Swart 2003). Others keep hunting dogs (Makwati et al. 2023), which may pose a threat to wildlife. As such, wildlife sharing space with humans is expected to keep safe distances away from human detection, as in many cases, wild animals may be viewed as a threat (Hermann and Menzel 2013).

Armadillos are generally understudied because of their elusive and nocturnal behaviour. As a result, information on their numbers and occurrence outside protected areas is scant. Therefore, the aim of this study was to determine landscape use and foraging behaviour of armadillos in a communal rangeland. The objectives were to determine: (1) the size (surface area and depth) and density of foraging burrows in different seasons, (2) the distance between active den entrances within a den, (3) the number of active and abandoned entrances at dens, (4) the location of the foraging areas in relation to the village, and (5) anthropogenic activity at the dens. We expected foraging burrows to be deeper and wider, and to increase in number in the wet season when prey are abundant. In addition, we expected more active and closely located den entrances for ease of escape and for armadillos to travel shorter distances from their dens to feeding sites in the communal landscape. We also expected hunting-related tampering at the dens.

MATERIALS AND METHODS

Study site

The study was carried out in the Ncunjane communal area (28°44'S, 30°27'E) of Msinga Local Municipality in the KwaZulu-Natal Province of South Africa (Fig. 1). Msinga is located in the upper basin of the Tugela River and is approximately 100 km from the

Indian Ocean to the east and the Drakensberg Mountains to the west (Fowler 2011).

Soil type and geology

The soil is shallow, reddish- brown and gravelly with limited amounts of clay and organic matter; thus, the region is relatively non-arable (van der Eyk et al. 1969), except for the floodplain of the Tugela River where crop farming occurs on some 840 ha (Cousins, 2013; Maziya et al. 2017). The area is noted for its steep slopes and rocky surfaces. Msinga comprises of broad alluvial plain (400–650 m asl) rising to the highveld north and south of the Tugela River (1200–1600 m asl) (Fowler 2011).

Vegetation and climate

The area is characterised by vegetation comprising bushveld and thornveld with sparse grass cover on rocky terrain (Fowler 2011). The grass layer consists of *Themeda triandra*, *Panicum maximum* and *Eragrostis curvula*, while the woody vegetation is dominated by deciduous trees such as *Vachellia tortilis*, *V. karroo* and *V. nilotica*, and evergreen trees such as *Olea europaea africana*, *Euclea crispa* and *Boscia albitrunca*

(Nzimande et al. 2022). Msinga receives a mean annual rainfall of 682 mm (Cousins 2013), that fluctuates between 400 and 900 mm (Mkhabela 2005) and most of this falls from December to February.

Sampling

Foraging burrow selection and classification

We sampled aardvark digging activities in the dry season (August 2020), rainy season (November 2020) and early dry season (May 2021). Sampling sites, as defined by aardvark activities, tended to be located on the outskirts (> 700 m) of the village. We identified areas of aardvark activity based on knowledge of the local people, who come across the sites while collecting firewood, poles or traditional medicines, or minding their livestock (cattle, goats and sheep), or hunting. We also searched through the village for aardvark activity and found none. We used 50 m × 10 m belt transects to quantify aardvark foraging burrows in each site of aardvark activity. We distinguished aardvark foraging burrows by claw marks, which were often evident on the sides of the burrow. In addition, burrows tended to have the tail of the aardvark outlined on the ground opposite the burrow with visible ant and/or termite

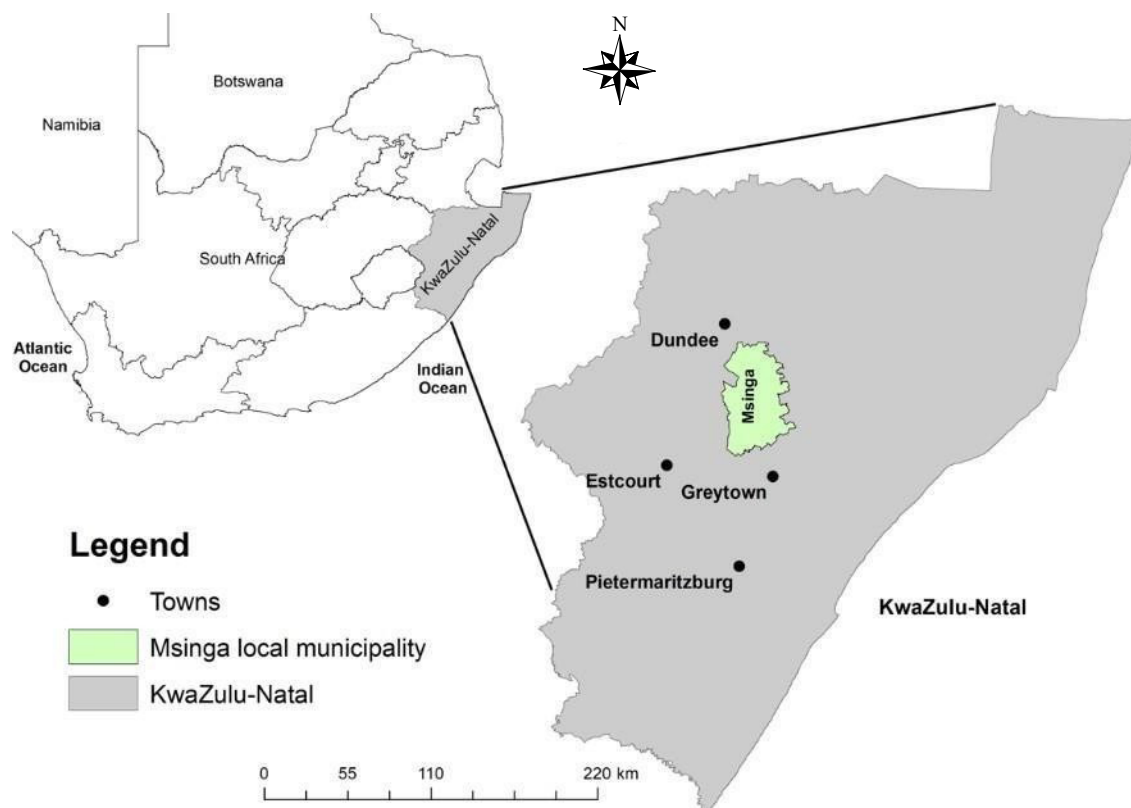


Fig. 1. Location of Msinga Local Municipality in the KwaZulu-Natal Province of South Africa.

tunnels where digging took place. We sampled from 23 transects across all seasons in two sites, which were located 1.74 km apart. However, only seven transects in the dry season showed recent foraging activity. Sampling followed sites of foraging activity. For each aardvark foraging burrow in each transect, we measured the maximum depth and two perpendicular lengths on the ground surface. We recorded the number of foraging burrows including those that were immeasurable because they were trampled by livestock and human movements. We qualitatively categorised the foraging burrows as new, old or very old (Fig. 2). New burrows showed evidence of recent soil disturbance, which resulted in the presence of a fresh mound and no plant growth on the mound. Old foraging burrows also had an absent or reduced mound and plant growth on previously disturbed areas. Additionally, very old foraging burrows tended to collapse thereby losing the characteristic shape and comprised of no mound, and mature and considerable vegetation cover in the foraging burrow.

Den sampling

Den and foraging burrow sampling took place simultaneously during the three seasons of sampling. We distinguished aardvark foraging burrows from dens by size. Specifically, foraging burrows are shallow with a maximum depth that can be seen, while burrows of dens are large and deep, and the end of the burrow is not visible from outside because it may be too deep (> 2 m depth) (Kingdon 2013; Kingdon et al. 2013), or the burrows are at an inclination from the soil surface, and also change direction. As such, dens were not measured but visually inferred. Dens were also characterised by several active and inactive/abandoned entrances. Most of the active dens were indicated by the presence of

unidentified flies (Order Diptera) around the entrance which follow the animal, and whose presence indicates a burrow system occupied by at least one aardvark. In addition, some active dens had newly deposited soil mound at the entrance of the den. Abandoned dens were old and further classified as collapsed in instances where the roof of the den broke or was no longer in use. We measured the size (length $\times$ width) of the dens on the ground surface from the farthest entrances on either side of the den. We also measured the distances between active den entrances within a den. We then counted the number of inactive or abandoned entrances. Additionally, we recorded the number of den entrances that were used for discarding refuse, e.g., disposable nappies. Also, we recorded den entrances covered with rocks that were placed by people to prevent their utilisation by snakes such as the Central African rock python (*Python sebae*). We also recorded burrows that were dug by aardvark hunters. We distinguished burrows dug by aardvark from burrows dug by hunters by their shape, angle and characteristics of the walls. For example, burrows made by hunters were vertical, less rounded, with flat walls showing evidence of the tool used in digging, such as a spade or shovel, while burrows dug by aardvarks are inclined at about $30\text{--}45^\circ$ from the ground surface, have claw marks on the walls, and may be partially covered by overhanging vegetation (Fig. 3). We measured the distance (m) from the foraging area to the closest den entrance across all seasons, which can indicate whether the animal sought to separate the foraging and refuge (den) areas. Furthermore, we were accompanied by one of the village hunters to give additional information on the patterns of aardvark activities in the village, and how many aardvarks they managed to catch over the eight months we conducted the study.



Fig. 2. Three different ages of foraging burrows of aardvark: (A) new hole with evidence of recent soil excavation and no plant growth, (B) old hole with mound of soil, and (C) very old hole with grass growth and no mound present. The metre rule is shown for scale.

Data analysis

We calculated the total number of foraging burrows, immeasurable foraging burrows, and aardvark and human-made burrows at dens using descriptive statistics. We further grouped immeasurable foraging burrows according to factors that affected them and season. All data were analysed using IBM SPSS Statistics for Windows version 27 (IBM Corp 2020). Burrow sizes were analysed statistically, while other data were analysed using descriptive statistics. The depth (cm) and surface area (cm²) of foraging burrows were compared among seasons (dry, wet and early dry) and age (new, old and very old). The area and depth were the dependent variables, whilst season and age were the independent variables. The data did not conform to normality after testing using a One-Sample Kolmogorov-Smirnov test, and no transformation could normalise residuals of the data. We then used generalised linear models which can be used for non-normally distributed data to determine if there were differences in the area and depth of foraging burrows among seasons and ages. Where significant ($P < 0.05$) the season and age treatments were further compared using a Bonferroni post hoc test. We used frequency of occurrence to present the materials found in aardvark foraging burrows and characteristics of active and abandoned dens. We used GPS points of active dens to calculate the distance between neighbouring dens. Dens that were > 1 km apart were regarded as independent and thus may have represented different animals. The number of animals was not accounted for in this study because we had no way to quantify it.

Ethical considerations

We obtained approval to conduct the study from the Mchunu Traditional Authority and ethical clearance with the ethics committee at the University of KwaZulu-Natal (HSSREC/00002877/2021 and AREC/016/020).

RESULTS

Foraging burrows ($N = 639$) were approximately 27 times more abundant than the dens ($N = 24$) during the three seasons of sampling in year 2020 and 2021. These occurred over an area of approximately 35 km². Specifically, we measured a total of 88 different-aged foraging burrows in the dry season, 276 in the wet season and 275 in the early dry season (Fig. 4). A total of 34 very old foraging burrows in the dry season, 34 in the wet season and 42 in the early dry season were immeasurable because of livestock trampling, human movements or were overgrown by grass. All seasons comprised a greater number ($> 51\%$) of old than new and very old foraging burrows (Fig. 4). New burrows increased in number in the wet and early dry seasons compared to the dry season.

The surface area of different-aged burrows differed significantly with season (Table 1; Fig. 5). The area of very old burrows in the early dry season was significantly greater than that of other burrows ($P < 0.001$). New burrows in the wet season were narrowest in area ($P = 0.028$). Similarly, the depth of different-aged foraging burrows varied with season (Table 1; Fig. 6). Different-aged burrows were similarly shallow in depth in the wet season, while new and very old foraging burrows were deeper than all foraging burrows in the dry and early dry seasons (Fig. 6).

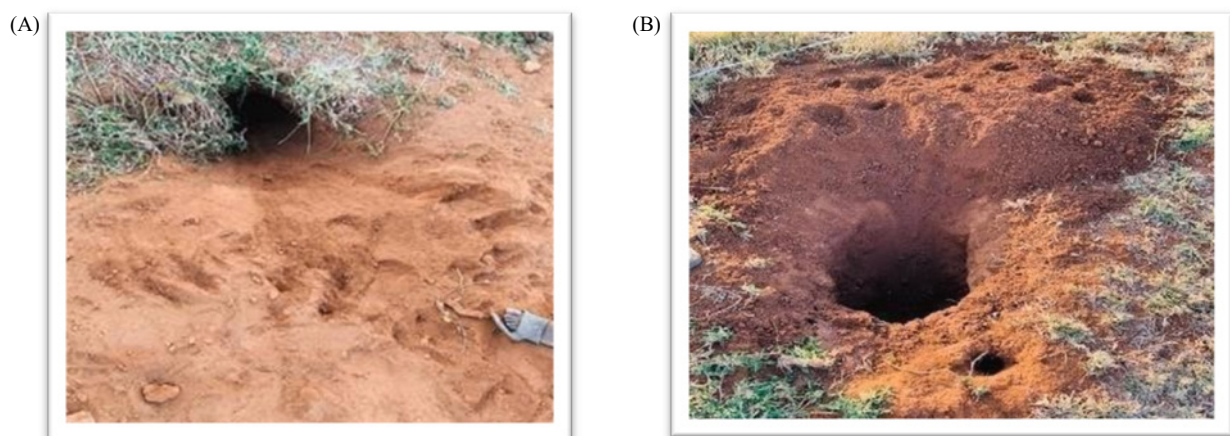


Fig. 3. (A) Aardvark active den with evidence of aardvark claw marks and fresh soil excavated on a new entrance to an old den, and (B) hole dug by hunters to catch aardvark with footprints of hunting dogs on the mound.

There were 91 active den entrances and 66 entrances not in use (abandoned) over the eight months. Hunters dug 15 new and 39 old dens over the eight months of the study and caught two aardvarks. One of the hunters indicated that an aardvark of a certain den

was caught and killed, leaving the den unoccupied for a while. However, we observed reoccupation of the same den. There were 18 den entrances closed with rocks by hunters or local people to block entrances of dens. In addition, a number of animals used aardvark dens

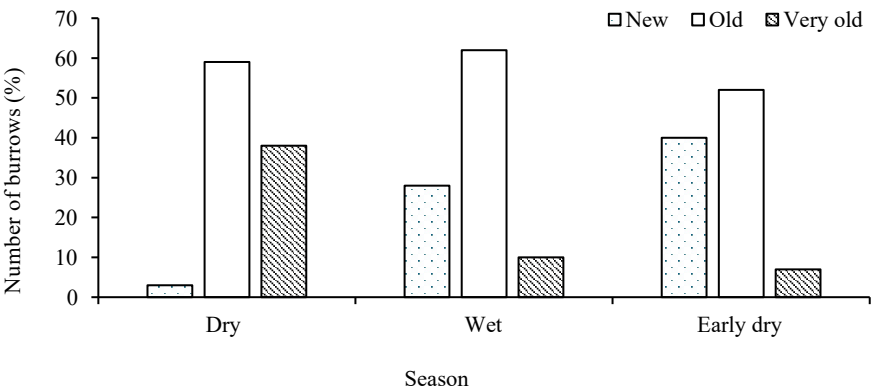


Fig. 4. Proportion (%) of different-aged foraging burrows across different seasons of the year 2020 and 2021 in Ncunjane, KwaZulu-Natal, South Africa.

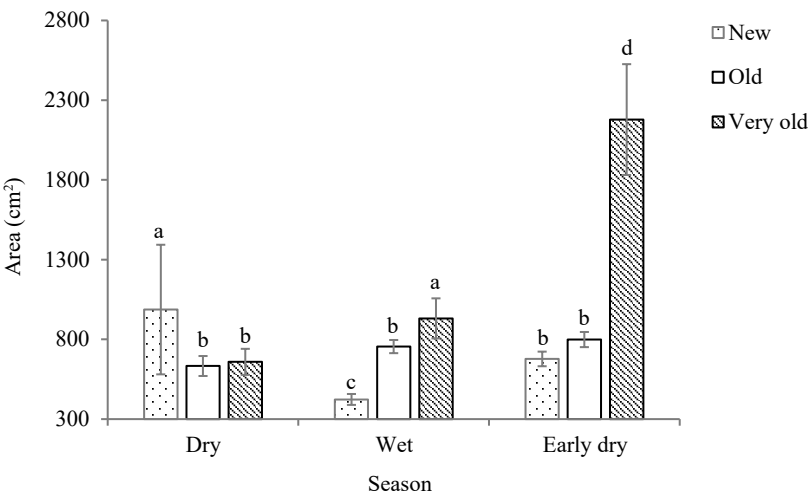


Fig. 5. Mean ($\pm$ SE) surface area (cm^2) of different-aged foraging burrows by season in Ncunjane, Msinga, KwaZulu-Natal, South Africa. Different superscript letters indicate significant differences ($P < 0.05$) among the age and season treatments.

Table 1. Wald’s chi-square values and associated probabilities for generalised linear models of the effects of season and age on the area and depth of aardvark foraging burrows in Msinga, South Africa. Significant p -values are shown in bold

Dependent variable	Independent variable	<i>d.f.</i>	Wald’s χ^2	<i>P</i>
Area	Season	2	20.71	< 0.001
	Age	2	23.20	< 0.001
	Season $\times$ Age	4	30.33	< 0.001
Depth	Season	2	89.12	< 0.001
	Age	2	7.54	0.023
	Season $\times$ Age	4	22.01	< 0.001

such as wildcats and Cape porcupines (Table 2). These were evidenced by faeces and quills, respectively. Also, humans used the dens to dispose of disposable nappies and plastic waste (Table 2).

The distance among active neighbouring den entrances was 0.5 km ($N = 14$; range: 0.1–1.0 km), 2.2 km ($N = 9$; range: 1.1–3.4 km) for abandoned dens and 2.9 km ($N = 5$; 1.7–3.9 km) for active independent dens. The average number of active entrances ($N = 4$) in each den was less than that of abandoned entrances ($N = 6$), and the distance between entrances within a den was 9.12 ± 1.07 m. Overall, we found 24 dens, 14 of which were active while 10 were abandoned. The aboveground size of active dens was 24 m $\times$ 20 m. The distance between the foraging area and nearest den during the dry season was 12.7 ± 0.7 m, while it was 61.0 ± 35.0 m in the wet season and 45.9 ± 37.2 m in the early dry season. Aardvarks fed closest to their dens in the dry season compared to the wet and early dry seasons.

DISCUSSION

Aardvarks occurred at the periphery of the village where their dens and foraging activities were evident. The area outside the human settlement was used for crop production and as a rangeland for livestock farming. Thus, habitat use by aardvarks in Ncunjane overlapped with human activities. Correspondingly, many very old foraging burrows were immeasurable ($N = 114$) due to livestock trampling and human activities. Facilitative effects of very old burrows on the landscape, such as plant regeneration, were unlikely to be realised due to disturbance and/or suppression by human and livestock activities. Yet, burrows with longer lifespans tend to have a significant impact on the regeneration of vegetation (Jones et al.1994). The extent of trampling by humans and other animals on foraging burrows is less severe than the acts of digging carried out on dens by hunters, which may destroy the den network and result in desertion of the den by the animal(s) (Makwati et al.

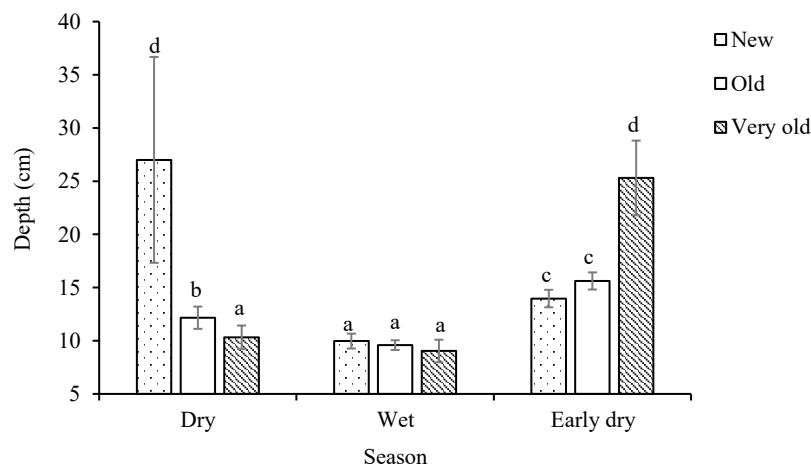


Fig. 6. The mean ($\pm$ SE) depth (cm) of foraging burrows across three seasons in Ncunjane, KwaZulu-Natal, South Africa. Different superscript letters show significant differences ($P < 0.05$) between the age and season treatments.

Table 2. Utilisation of active ($N = 16$) and abandoned ($N = 7$) entrances of aardvark dens over eight months in Ncunjane, KwaZulu-Natal, South Africa

Content	Number of entrances utilisation
#Snake	2
Spider web	28
Disposable nappies	1
Plastic waste and other rubbish	4
Cape porcupine	4
Rocks	18
Snare (sticks and wire)	2
Ashes and used charcoal	1
Wildcat faeces (<i>Felis silvestris/lybica</i>)	1

#An African rock python and a Mozambique spitting cobra (*Naja mossambica*) were observed entering aardvark dens during the sampling period.

2023). It was common to come across animal dung in the different-aged burrows, which further indicated use of the rangeland by domestic animals. Livestock dung captured in the burrows can influence seed germination (Dean and Milton 1991). In addition, we found the foraging areas of aardvarks to be located close to dens, which would limit the distance they travelled in the rangeland. Aardvarks in Ncunjane may thus be limited in their movements compared to their counterparts occurring in protected areas, where they are reported to travel distances of up to 4 km a night (van Aarde et al. 1992). Aardvarks may adjust movement patterns to avoid humans and their domestic animals such as dogs.

As predicted, the present study showed that foraging burrows in the wet season were approximately 12 times more abundant compared to dens over the eight months. This likely coincided with an increase in termite prey availability (Taylor et al. 2002; Kingdon et al. 2013; Kanyi et al. 2021). These results were similar to those reported by Martin (2017), which showed that foraging burrows were 15 times more abundant than dens in one season of data collection at Samara Private Game Reserve in the Eastern Cape Province of South Africa. The findings were expected as aardvarks occur at low densities (Kingdon et al. 2013). In addition, one aardvark can have a significant impact on the landscape, as Taylor et al. (2002) indicated that aardvarks dug up to 200 foraging burrows per night. As such, foraging burrows may play a greater ecological role across landscapes than dens due to their high abundance.

The variation in number of foraging burrows in each season could be attributed to the availability of ant and termite prey. Ants and termites were observed on the soil surface in the wet and early dry seasons, which agreed with the extent of digging foraging burrows by aardvarks (van Aarde et al. 1992; Taylor and Skinner 2003), thus the two seasons recorded a significant number of foraging burrows. In contrast to expectation, aardvarks dug new, shallow foraging burrows in the wet season presumably because their prey was available near the surface where the soil was less likely to be saturated with water (Davies et al. 2015). Despite this, the relative abundance of the foraging burrows was greater in the wet season. Conversely, we recorded wider foraging burrows in the early dry season, which likely presented scarcity in termite prey, as they settle belowground in the dry season (Braack 1995). The increase in size of foraging burrows might also indicate increased search effort to find food. In addition, Taylor et al. (2002) showed that aardvarks dug foraging burrows of 5–10 cm for ants and up to 2 m for termites but foraging burrows in Ncunjane were shallow (≤ 27 cm). The shallow foraging burrows may suggest that aardvarks in this study area fed predominantly

on ants or that the termites were available close to the surface. Thus, food availability associated with season influenced the variation in digging effort.

Consistent with findings of other studies, we found that abandoned dens were used by animals other than aardvarks (Whittington-Jones et al. 2011; Pike and Mitchell 2013). Spiders used old foraging burrows and den entrances probably for refuge, capture and nesting sites. Therefore, the results showed that foraging burrows also provide refuge and nesting sites to other animals including invertebrates. People interfered with the dens by placing rocks to close den entrances because large snakes such as pythons can utilise them. The measure was an attempt to keep large snakes away from people. Contrary to expectation, we recorded fewer active compared to abandoned entrances in the den systems. A similar pattern was reported in protected areas (Taylor et al. 2002). In addition, the distance between active den entrances in a den was short with several entrances, presumably, to facilitate escape routes in the human-dominated landscape. The neighbouring dens could be used by the same aardvarks because they have been reported to have a home range of 180–350 ha (Van Aarde et al. 1992), and aardvarks do not share their dens (Taylor et al. 2002; Taylor and Skinner 2003). As such, the dens, which were located over 1 km from each other likely represented different animals. The size of the dens were large in Ncunjane compared to a protected area in the Karoo, South Africa (Taylor and Skinner 2003). This could suggest limited suitable space for aardvarks or habitat preference.

People in our study area used aardvark dens as sites for waste disposal, which may have encouraged aardvarks to abandon the den. In addition, the evidence of snares, hunter diggings and ashes from fires set to smoke out aardvarks from dens showed that aardvarks are persecuted by people in Ncunjane (Makwati et al. 2023). Thus, the most severe impact by humans on aardvarks is hunting, which likely contributed to an increased number of abandoned dens, and lower aardvark numbers. Therefore, aardvarks face threats from local people, which is a consequence associated with co-existing with humans, which in turn threatens their future occurrence in the area. The use of the landscape by aardvarks is influenced by prey availability (Taylor et al. 2002; Taylor and Skinner 2004) but may also be limited by human activities and hunting as shown in this study. Conservation of wildlife should extend beyond protected areas.

CONCLUSIONS

The unique situation of proximity to humans likely

influenced the movement patterns and landscape use by aardvarks in Ncunjane. It seemed to have influenced distance to feeding sites, which were shorter than recorded in protected areas. We recorded no evidence of feeding within the village, which likely showed clear avoidance of the space of increased human activity. The size of aardvark dens was also larger than reported in protected areas. There were also several dens located within short distances (≤ 500 m), which may be used by the same individuals to avoid threats or indicative of confinement dictated by human activities. We also showed, probably for the first time, that people use aardvark burrows for dumping disposable nappies and rubbish. People also avoid snakes by closing dens near human settlements. Sharing the rangeland with local people likely affected how aardvarks used the landscape and their movement patterns. Wildlife awareness and conservation efforts should incorporate rural areas.

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Competing interests: NT, MK and ZT declare that they have no competing financial or personal interests.

Availability of data and materials: The data are available upon request.

Consent for publication: Participants consented to participate in the study.

Ethics approval consent to participate: Not applicable.

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