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Burrow site selection in the Sungazer (*Smaug giganteus*): a threatened South African endemic lizard

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ABSTRACT

Elucidating factors that drive microhabitat selection in a species is important for informing the conservation management of the species. For species that use microhabitats as long-term refuge sites, selection pressures are likely to be strong because the microhabitat must fulfil their eco-physiological and life history requirements. *Smaug giganteus* (Sungazer) is a threatened (Vulnerable) cordylid lizard species in the highveld grasslands of South Africa – a key agricultural area in the country. Individuals dig burrows as refuges, which increases their sensitivity to habitat transformation. In addition, previous attempts to translocate populations have failed due to a lack of knowledge about their specific microhabitat requirements. We assessed microhabitat characteristics that may influence burrow site selection by measuring vegetation characteristics surrounding Sungazer burrows and comparing these to vegetation at randomly selected sites. We also recorded orientation, aspect, soil composition, and the presence of other animal dung. Sungazers selected sites with sparse vegetation cover, and where grass height was short, but had no preference for soil composition. There was no relationship between the presence of ungulate dung and the placement of Sungazer burrows. Most Sungazer burrows were orientated in a northerly direction on north-facing slopes, suggesting that burrow placement has thermoregulatory advantages. We recommend that to identify suitable sites for Sungazer translocations, landscapes are thoroughly surveyed with cognisance to the findings in this study, and that a soft-release translocation protocol follows to maximise translocation success.

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Introduction

Many animals use environmental factors to select habitats or microhabitats. Appropriate selection of habitats and microhabitats may result in improved body condition (Stark et al. 2022), better foraging and thermoregulation opportunities (Huey et al. 1989; Perry and Garland 2002; Whitaker and Shine 2003), appropriate conditions for nest construction (Huey et al. 1989; Kolbe and Janzen 2002), and protection against predators (Kacoliris et al. 2010). Careful choice of these factors is particularly important for ectothermic

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animals, such as reptiles, whose physiologies are strongly influenced by the environments in which they live (Huey 1991; Vitt and Cadwell 2013). Selective pressure on the choice of optimal ambush and retreat sites is particularly important for animals that use those sites as a permanent refuge, because food and shelter are critical for their survival. Knowledge of the factors that animals use to select those permanent refuges can thus be critical for their conservation management.

Vegetation structure and cover are key factors that influence microhabitat choice in reptiles (Dias and Rocha 2004; Kacoliris et al. 2010; Masterson et al. 2008). Some species prefer highly vegetated microhabitats, while others prefer reduced cover (Dias and Rocha 2004). In such instances there are differences in how these microhabitats are used. For example, species living in highly vegetated areas may have reduced activity periods due to limited sunlight availability (Dias and Rocha 2004). Reduced vegetation cover may also promote early visual detection of predators, which may be important for habitat specialists that remain close to refuge sites. By contrast, increased vegetation cover could provide generalist species with a network of hiding places to escape predation (Kacoliris et al. 2009). Open microhabitats may offer better basking opportunities for thermoregulation (Whiting et al. 1993), while increased vegetation cover and certain types of vegetation may provide shaded patches and microclimates to facilitate shuttling between basking sites and shade (Song et al. 2017; Warner 2023). From a foraging perspective, reduced vegetation cover caused by grazing animals may result in dung, which attracts invertebrates (Atkinson et al. 2004). Thus, vegetation structure and cover offer a range of benefits and consequences, and selection for a particular microhabitat is likely influenced by a species' eco-physiological requirements.

Many reptiles seek refuge in burrows that are often interspersed within the landscape. Seeking refuge or shelter in burrows not only provides a stable thermal environment (Warner 2023), but also offers protection against physiological (e.g. thermoregulation and water loss), ecological (e.g. protection against predation) and environmental (e.g. heat and aridity) extremes (Williams et al. 1999). For species that construct their own burrows and use them as long-term or permanent refuge sites (e.g. the Sungazer, *Smaug giganteus*; Van Wyk 1992), selection of appropriate sites to construct burrows may particularly be driven by characteristics of the vegetation cover, soil type and soil composition (Jones and Dorr 2004; Naderi et al. 2011). In such instances, careful selection of the direction in which to orientate burrow entrances may also be necessary to assist with thermoregulation (Pianka and Giles 1982; Song et al. 2017). For species with social structure, selection of suitable microhabitats in which to construct burrows may also be influenced by the abundance of these microhabitats within the landscape. Thus, there is likely to be strong selective pressure for choosing appropriate sites to construct burrows, presumably because these sites need to continuously offer physiological and ecological benefit across multiple scales.

Despite the eco-physiological and evolutionary constraints associated with microhabitat selection and habitat use, anthropogenically driven threats, such as land transformation, overgrazing, crop-ploughing, industrial development and poaching (Masterson et al. 2009; McIntyre and Whiting 2012; Parusnath et al. 2017), may further constrain selection and use of suitable habitats. Transformed habitats not only reduce the number of available suitable microhabitats for some species, but may also alter thermal environments (Nowakowski et al. 2018), change predation risk (Pietrek et al. 2009), influence

behavioural patterns (Wasiolka et al. 2009), limit dispersal (Nowakowski et al. 2013), thus altering the population dynamics of a species (Gardner et al. 2009). These factors can be detrimental to the conservation of species, especially for habitat specialists and those that are already threatened.

The Sungazer (*Smaug giganteus*) is a threatened (Vulnerable; Alexander et al. 2022), heavily armoured lizard species that is endemic to the Highveld grasslands of South Africa (De Waal 1978; Jacobsen et al. 1989; Van Wyk 1992). Sungazers are large-bodied (snout–vent length (SVL) of ~ 180 mm; Van Wyk 1992; McIntyre 2006) lizards that live for more than 21 years in the wild (Stanton-Jones et al. 2023). Unlike most other species in the Cordylidae, they use self-constructed burrows in the grassland mosaic as long-term refuges (Van Wyk 1992). Sungazers are strict ambush foragers that feed, almost exclusively, on arthropods (Van Wyk, 2000), and activity is mainly in close proximity to the home burrow (within a 2 m radius; Van Wyk 1992; Ruddock 2000). This philopatric lifestyle suggests that Sungazers select microhabitats in which to construct their burrows. However, since the Highveld grasslands support extensive agricultural and mining activities (DEAT 2005; McIntyre 2006), Sungazer subpopulations are susceptible to decline because of habitat transformation and fragmentation (Van Wyk 1992; McIntyre and Whiting 2012; Parusnath 2014). Thus, comprehensive knowledge on how Sungazers are selecting microhabitats in which to construct their burrows is necessary to inform decision making for translocation protocols, especially considering that previous translocation attempts appear to have been unsuccessful (Groenewald 1992; Parusnath 2014).

In this study, we identified some of the factors that potentially drive burrow site selection by Sungazers within the grassland matrix, and recorded some important burrow metrics. We compared microhabitat characteristics directly around each burrow to nearby random sites available in the surrounding landscape. This assessment was carried out at the broadscale population level. Because of anecdotal evidence from field observations, and because Sungazers exist in an agricultural landscape where the abundance of grazing animals can be high, we predicted that Sungazer burrows would be associated with habitat patches consisting mostly of short vegetation, where the abundance of dung left by grazing animals is high and therefore, may increase foraging opportunities (Atkinson et al. 2004). We also predicted that Sungazer burrows would occur in sandy soils, which may facilitate burrow construction (Jones and Dorr 2004). Finally, we predicted that most burrows would face northwards and would occur on north-facing slopes because these slopes may offer thermoregulatory support (Barton et al. 2019). Knowledge of the factors influencing burrow site selection in Sungazers may not only facilitate future surveys, but provides information to enhance conservation management plans for this vulnerable species.

Materials and Methods

Study site

We surveyed 24 sites within the geographic range of the Sungazer between November 2019 and December 2022. These sites were located across the eastern, central, and western regions of the Sungazer distribution within the Free State province, South Africa. Specifically, the sites were located near the towns of Heilbron, Petrus Steyn,

Kroonstad, Welkom, Senekal, Lindley, Harrismith and Vrede. These regions were selected to ensure that data from major parts of Sungazer distribution were collected. All sites fall within the Highveld Agricultural Region of South Africa (DEAT 2005) and are situated within the grassland biome (Van Wyk 1992; Parusnath 2014). These grasslands comprise a patchwork mosaic of dense grasses interspersed with areas of open vegetation or bare ground, amongst which Sungazer burrows are usually located (Figure 1). Because Sungazers are a threatened species, we have not shared the precise locations of the field sites based on the recommendation by the South African National Biodiversity Institute (http://nssl.sanbi.org.za/).

Field sampling

We located 106 burrows across 24 different Sungazer aggregations. We defined an aggregation of Sungazers as a cluster of Sungazer burrows existing within a study site. Although we attempted to locate at least five Sungazer burrows from each aggregation, in some cases only two burrows were located due to low Sungazer abundance at those sites. Sungazer burrows are identifiable by their kidney-shaped entrance, and a bare patch of earth leading towards entrances (Figure 1a.; Van Wyk 1992). To assist with locating Sungazer burrows, we used burrow records from previous studies (e.g. McIntyre 2006; Parusnath 2014; Stanton-Jones 2018). At sites where Sungazers had not previously been recorded we walked line transects, 5 m apart, to find Sungazer burrows. Occasionally, burrows were opportunistically found. The coordinates of each burrow were recorded using a handheld GPS (Garmin GPSMAP 78s). To assess which factors influence burrow site selection in Sungazers, we recorded the following attributes within a 4 m^2 quadrat centred on each burrow: (1) burrow orientation using compass reference points, (2) land aspect (slope orientation) according to compass reference points, (3) a visual estimation of the percentage of vegetation cover greater than 100 mm in height (vegetation cover); (4) mean height of vegetation, and (5) number of animal droppings (typically large herbivores, and excluding droppings from Sungazers). We measured vegetation height at three different points, from the shortest to the tallest vegetation, within the quadrat to calculate a mean value.

We initially assessed each Sungazer burrow for occupancy by inspecting whether the entrances were clean from debris and cobwebs, or if Sungazer scales, claw marks or tail



Figure 1. An active Sungazer burrow (a), grassland mosaic showing bare open patches amongst denser areas of vegetation (b) and a Sungazer basking amongst short patches of vegetation outside its burrow (c).

marks were present at the entrance. We verified Sungazer presence by inserting a Bosch borescope camera (Bosch GIC 120 C) down each burrow. To assess if Sungazers construct their burrows in specific microhabitats within the grassland mosaic, we measured microhabitat attributes within an equal number of 4 m^2 quadrats at random locations at each study site. Random points were located by spinning a pencil at a confirmed Sungazer burrow and letting it fall to the ground to determine the direction to the random point. We then used a random number generator to produce a number between 10 and 100 and walked the resulting number of paces in the direction indicated by the pencil. Each Sungazer burrow was therefore paired with a random site within the habitat to facilitate a comparison of where Sungazers were found to where they were not. A similar approach has been used in other studies and has yielded successful results (e.g. Schlesinger and Shine 1994; Quirt et al. 2006).

Soil parameters

Since the composition of soil may affect where burrows are constructed, the coordinates of each study site were overlayed onto a soil composition map (scale = 1: 2 000 000; Batjes 2004) of South Africa in QGIS (Version 3.26.0). The soil composition map provides soil parameter estimates for depths of 0.2 m to 1 m (Batjes 2004), giving an indication of what the composition of soils within Sungazer habitat is at a broadscale level. We then extracted and recorded the components of soil composition (% sand, % silt, and % clay) associated with each Sungazer aggregation. To compare these parameters against sites where Sungazers do not occur (i.e. outside of the Sungazer geographic range), we used QGIS (Version 3.26.0) to generate an equal number of random points ($n = 24$) between the Sungazer's interpreted distribution and its extent of occurrence (EOO) and extracted and recorded the soil composition at each point.

Statistical analyses

Soil parameters

To assess whether Sungazer burrows persist in habitats characterised by a certain soil composition, we conducted Mann-Whitney U tests and compared each soil parameter (sand, silt and clay content) associated with Sungazer aggregations to those at random locations. We did this because our data for soil composition did not follow a paired design and did not meet the assumptions of normality, even after the arcsine square root transformation was applied. Thus, since nonparametric testing was used, the median values for each soil component is reported in our findings. It is also important to note that the geographical scale of the soil composition map used to extract the measures of each soil component allowed for a broadscale assessment of soil composition between Sungazer habitat and nearby random sites, and thus the analysis is unlikely to detect fine scale differences in soil composition. Nevertheless, the assessment provided a broadscale indication of the soil composition in which Sungazers occur.

Site attributes

Burrow orientation data were summed according to the aspect of the land in which burrows occurred, and a Pearson's Chi-square test was performed to test for association

between the two variables. For this analysis, we excluded two burrows that appeared to occur on flat ground and could not easily be assigned an aspect to the land slope. The remaining microhabitat characteristics associated with Sungazer burrows and random sites were tested for normality using the Shapiro-Wilk test. We also excluded outliers from our analyses for vegetation cover, and vegetation height, as these datapoints probably existed due to sampling error. Apart from vegetation height, the other variables did not meet the assumptions of normality even after application of the appropriate transformations (arcsine square root transformation for proportion estimates, and log transformations for the remaining variables). Thus, because our analysis followed a paired design, we used a dependent *t*-test for vegetation height, and Wilcoxon signed-rank tests for the remaining variables to test for differences in each microhabitat characteristic between Sungazer burrows and random sites. To reduce the risk of Type I error through multiple testing, a Bonferroni correction was applied to the analyses (Armstrong 2014). Where non-parametric tests were used, the median values for microhabitat characteristics are reported. All statistical analyses were performed using the default statistics packages in *R* 4.1.1 (R Core Team 2021).

Results

Soil parameters

We found no significant difference in the amount of sand ($W = 246$, $p = 0.38$), silt ($W = 324$, $p = 0.45$) and clay ($W = 364$, $p = 0.11$) between Sungazer aggregations and random sites. However, sand content was the highest component of soils at random sites (Median = 57%) and at Sungazer aggregations (Median = 65%; Figure 2). Clay and silt content at random sites and Sungazer aggregations were comparatively lower than sand content with median values in the range of 18–22% (Figure 2).

Site attributes

Burrow orientation and land aspect

Of the 106 recorded Sungazer burrows, the majority (58%) of entrances were north, north-east, or north-west facing (hereafter, northerly orientations). By comparison, only 26% of burrow entrances faced south, south-east, or south-west (hereafter, southerly orientations), and 16% of burrow entrances faced east or west. There was a significant association between the orientation of burrow entrances and land aspect ($X^2 = 103.22$, df = 49, $p < 0.05$), with most burrows orientated in northerly directions being situated on north facing slopes (75%; Figure 3). Although burrows that are not orientated in northerly directions appear to be randomly distributed across different slopes, approximately 50% of southerly orientated burrows also occurred on south facing slopes (Figure 3).

Microhabitat characteristics

Percent vegetation cover was significantly lower at Sungazer burrows than at paired random sites ($V = 143.5$, $p < 0.001$), with a median value for vegetation cover at burrows and random sites of 10% and 65%, respectively (Figure 4). Sungazer burrows were also associated with significantly shorter vegetation compared to random sites

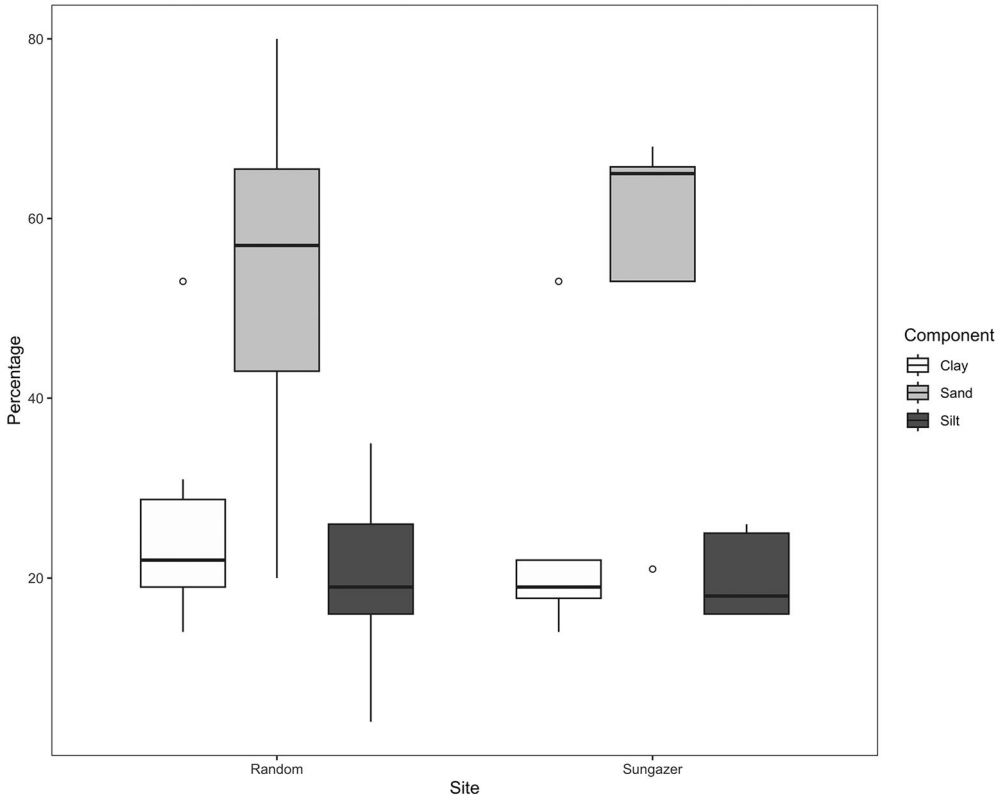


Figure 2. Boxplots showing the soil parameter estimates (%) of clay, sand, and silt content at Sungazer aggregations ($n = 24$) and random sites ($n = 24$). Random sites were situated between the Sungazer's geographic range and its extent of occurrence. Open circles depict outliers in the dataset.

(*t*-test, $t = -8.7$, $p < 0.001$)). The mean (± standard deviation (SD)) height of vegetation at Sungazer burrows was 205.7 ± 69.4 mm compared to 289.1 ± 109.6 mm at random sites (Figure 5). There was no significant difference in the number of animal droppings between Sungazer burrows and random sites ($V = 1456.5$, $p = 0.87$), but many outliers were present in the dataset (Figure 6).

Discussion

Sungazers construct their burrows in areas of short grass with sparse vegetation cover (Figure 1). By comparison, random sites within the landscape were associated with higher vegetation cover with tall and dense grasses. Sungazers do not appear to have an obvious preference for a particular soil composition since we did not detect any differences in soil composition at burrows and random sites. However, it is possible that we did not detect small scale differences due to the assessment being conducted on a fairly broad scale. When constructing their burrows, Sungazers typically orientate burrow entrances according to the aspect of the slope, in north-facing directions. Although only a limited number of attributes of Sungazer burrows and microhabitat characteristics were assessed in this study, our findings revealed that there is preferential selection for

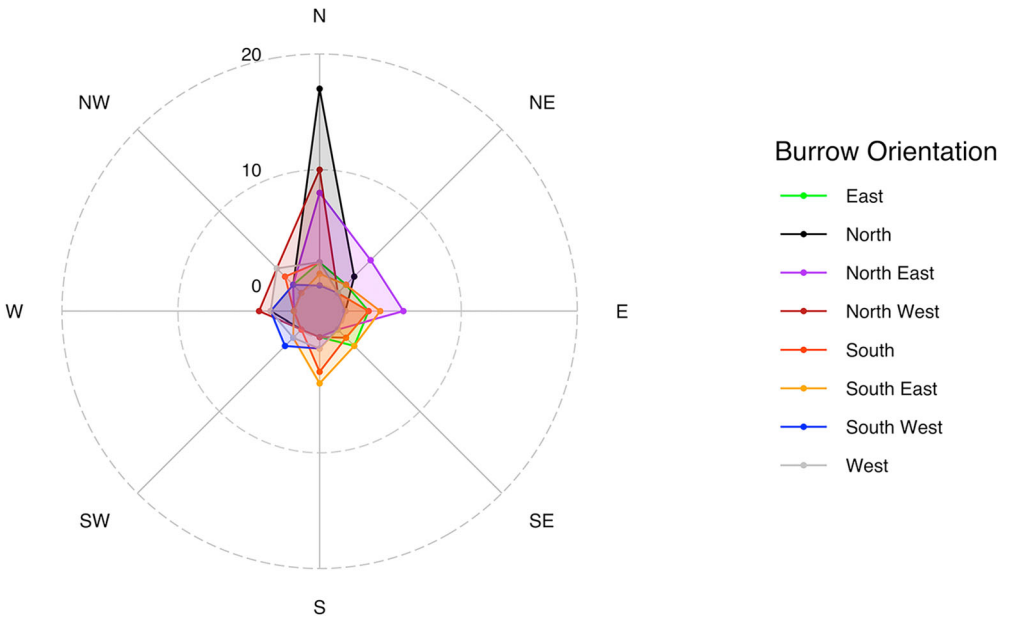


Figure 3. Radar chart showing the number of Sungazer burrows ($n = 104$) and the orientation of their entrances in relation to the aspect of the land slope. The gridlines on the chart represents the slope aspect while each point depicts the total number of burrow entrances facing a certain orientation at the slope aspect. Aspect and burrow orientations were assigned according to compass directions.

microhabitats with particular characteristics for burrow sites. This selectivity provides valuable information to future Sungazer population surveys and translocation protocols.

The majority of Sungazer burrows were found in regions of the landscape with sparse vegetation cover, supporting our initial predictions. This suggests that Sungazers select fairly open areas with short vegetation and grasses to construct their burrows. This may be because of the eco-physiological advantages that these microhabitats offer. Because Sungazers thermoregulate near their burrows by adjusting body posture and orientation (Stanton-Jones et al. 2018), dense vegetation and increased cover may increase the size of shaded patches and prevent lizards from thermoregulating effectively. Open bare patches of ground leading up to entrances may also be warmer due to increased exposure to the sun's rays (e.g. Whiting et al. 1993). Thus, reduced vegetation cover may facilitate behavioural thermoregulation in Sungazers by increasing access to direct sunlight. The ability to detect predators (e.g. birds of prey, small mammals, and some snakes; landowners, pers. comm.) may also be limited in densely vegetated habitats. Therefore, having their burrows situated in habitat patches with reduced vegetation cover may assist Sungazers with escaping predation since predators cannot easily approach unobserved. From a foraging perspective, Sungazers commonly prey upon arthropods (Van Wyk 2000), and thus low vegetation cover may also enhance prey detection and acquisition. These advantages may be particularly important for Sungazers given their sedentary lifestyle and periods of activity occurring within close proximity to their burrow entrances (Van Wyk 1992; Ruddock 2000; Stanton-Jones 2018).

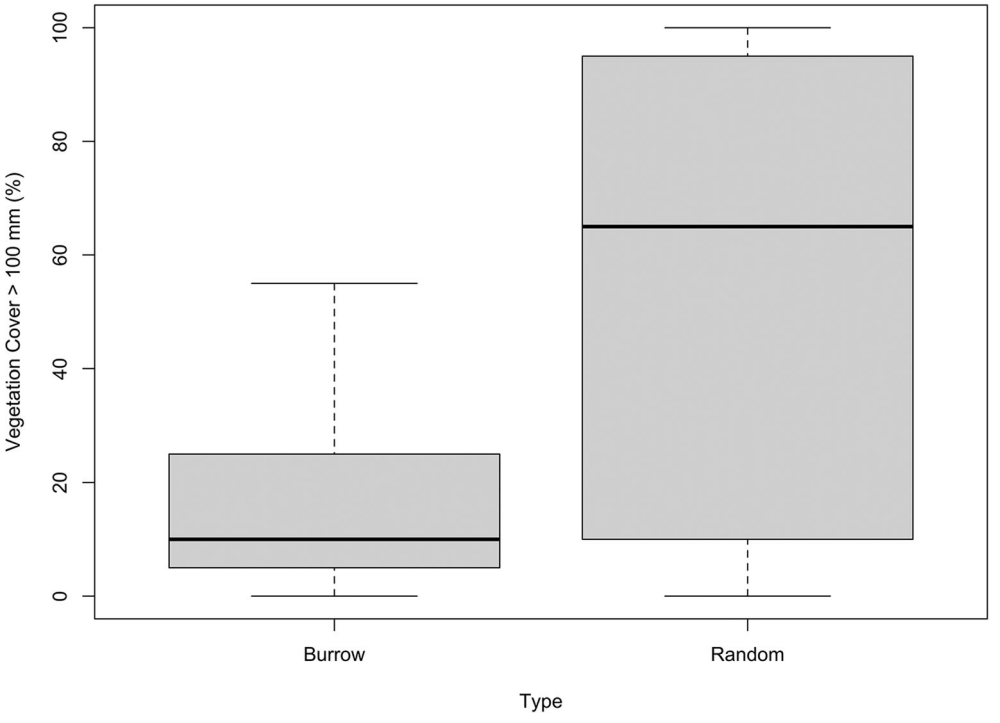


Figure 4. Boxplots comparing the estimated percentage of vegetation cover (> 100 mm vegetation height) within 4 m^2 quadrats of Sungazer burrows ($n = 97$) and random sites ($n = 97$).

The factors causing patches with reduced vegetation cover goes beyond the scope of this study. However, the habitat in which Sungazers occur likely consists of suitable grasses for grazing cattle and other game. These animals may be reducing the vegetation cover in the landscape providing ideal microhabitats for Sungazers. For example, McIntyre (2006) recorded over 70 Sungazer burrows at a single farm where there was a high abundance of grazers, and the site was considered overgrazed. Although the high number of Sungazers at this site suggests a possible symbiotic relationship between Sungazers and grazing animals, the factors driving reduced vegetation cover and short grasses within Sungazer habitat remains unknown. However, our findings, and the large size of the Sungazer subpopulation reported in McIntyre (2006), suggests that Sungazers are taking advantage of microhabitats with reduced vegetation cover.

In general, Sungazers preferentially select north-facing slopes on which to construct their burrows. This is not surprising since these slopes offer higher levels of direct solar radiation (Barton et al. 2019), likely facilitating basking activities (Van Wyk 1992). Sungazers also construct their burrows with entrances facing in the same direction to which the land slopes. Although a similar finding has been reported by Branch and Patterson (1975), and Jacobson et al. (1990), and has been linked to Sungazer thermoregulation (Van Wyk 1992), there may be additional ecological benefits associated with orientation selection. Our anecdotal observations from the field suggests that burrows orientated with slope aspect may also assist with drainage during thunderstorms. However, more studies relating burrow orientation and land aspect to burrows flooding and drainage are required to

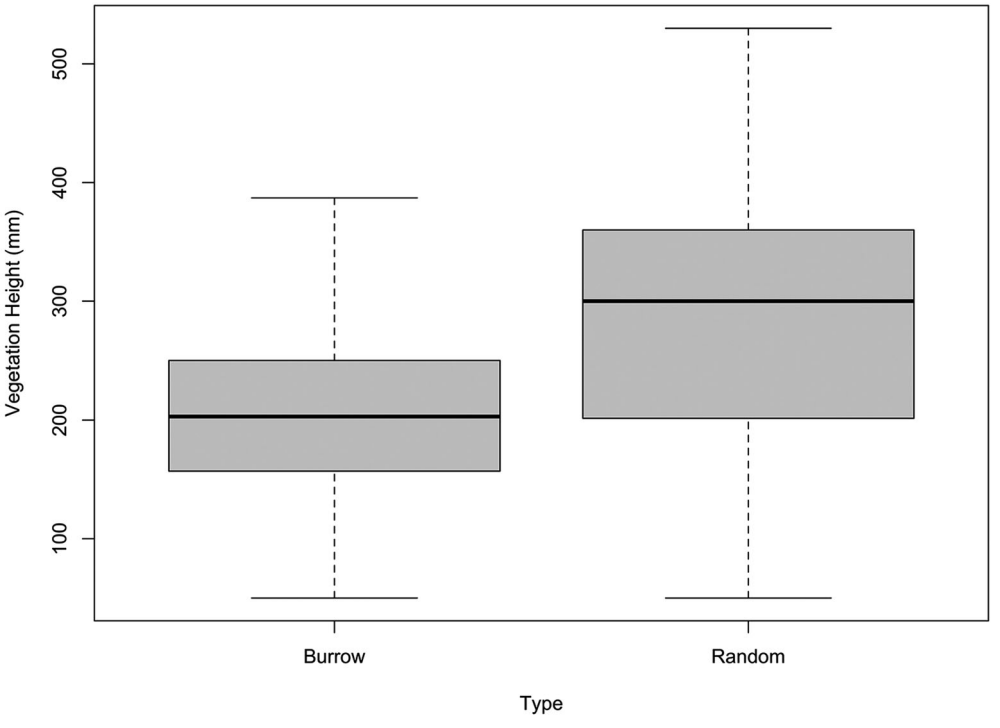


Figure 5. Boxplots comparing the height of the vegetation within 4 m^2 quadrats of Sungazer burrows ($n = 100$) and random sites ($n = 100$).

test this hypothesis. Nevertheless, there does appear to be physiological and ecological benefits to Sungazers by having their burrows orientated with slope aspect.

Preference for orientating burrow entrances towards a particular direction appears to be species dependent. For example, the Australian *Liopholis inornata* (Desert Skink) has a preference for orientating the entrances of their burrows in northerly directions, while *Liopholis striata* (Night Skink) favours southerly directions for their burrow entrances (Pianka and Giles 1982). Most Sungazer burrow entrances in our study were also in northerly directions, suggesting that preference for a particular orientation may be driven by thermoregulatory demands. This may also be justified by the strong association between the aspect of the slope and Sungazer burrow orientation. Importantly, Sungazers differ to some *Liopholis* spp. in that they are diurnal lizards that only construct a single entrance to their burrows where some *Liopholis* spp. are nocturnal and may construct a few burrow entrances (Fenner et al. 2012). This suggests that in order to facilitate thermoregulation, slope selection and a preference to orientate burrow entrances with the slope aspect may be particularly important for Sungazers.

There was no statistical difference in the number of animal droppings at Sungazer burrows compared to random sites, which was unexpected. Since it is not uncommon to find grazing ungulates in Sungazer habitat, we expected Sungazers to select sites where grazing frequently occurs as dung left by grazing ungulates may attract invertebrates (Atkinson et al. 2004), providing Sungazers with a food resource benefit (van Wyk 1992). However, while this may be plausible in landscapes where game occurred

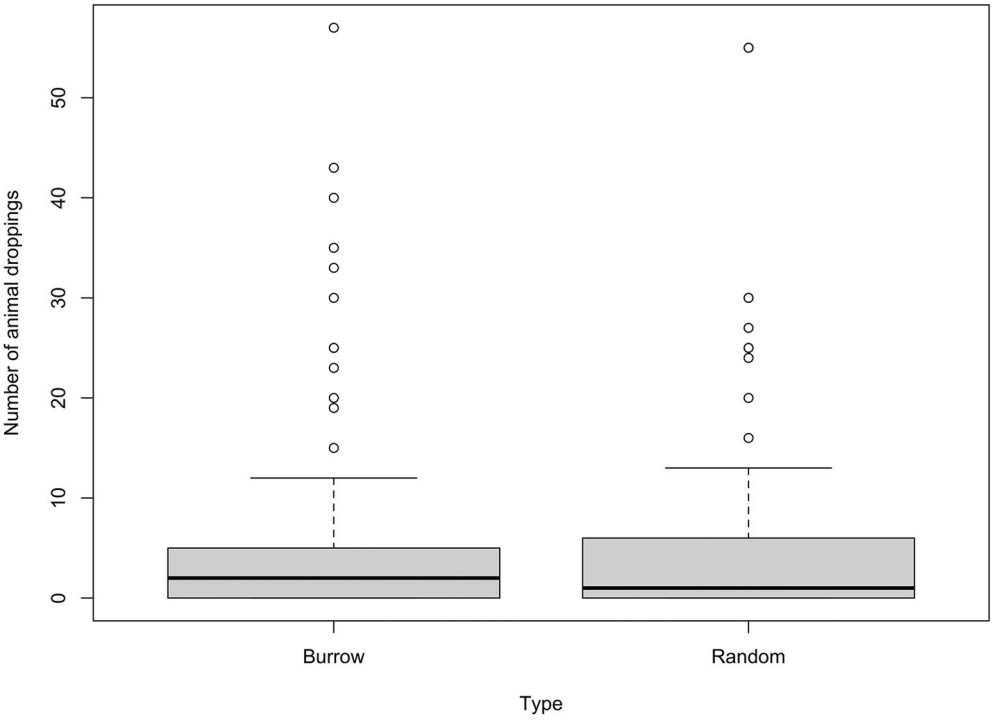


Figure 6. Boxplots comparing the number of animal droppings within 4 m^2 quadrats of Sungazer burrows ($n = 106$) and random sites ($n = 106$). Open circles depict outliers in the dataset.

historically, it is unlikely the case in the modern era since many cattle farmers have rotational grazing regimes and dung may therefore be scattered throughout grazing habitats, areas in which only a fraction of Sungazer subpopulations occur. Thus, while dung may facilitate foraging opportunities for Sungazers, and since high quantities of dung may exist near some Sungazer burrows, it appears to be coincidental and suggests that burrow site selection by Sungazers may not be driven by the abundance of animal droppings.

This is the first study to quantitatively assess characteristics of the microhabitat associated with Sungazer burrows. By using a paired design, a direct comparison of microhabitat characteristics between Sungazer burrows and random sites was made, contributing to our knowledge of the factors that may influence burrow site selection by Sungazers. However, there were a few limitations to the study. Even though this study has provided an indication of soil composition associated with Sungazer habitat at a broad scale, no small-scale link between soil composition and Sungazer burrows could be made. A more comprehensive dataset of soil characteristics (e.g. temperature, moisture, fine scale soil composition) of Sungazer burrows and random sites would enhance our knowledge of Sungazer ecology and behaviour. When collecting data on the number of animal droppings around Sungazer burrows and random sites, the data revealed many outliers. Although these outliers may be explained by samples being collected on farms with a high abundance of grazers, they still have statistical implications in that no clear trend in our findings can be detected, and therefore we caution against overinterpretation of

our finding of a lack of difference. In addition, our study focused on the vegetation density surrounding Sungazer burrows, and while the findings are valuable for conservation management of the species, the species composition of the grasses surrounding Sungazer burrows may also be important. Despite these limitations, this study has revealed some of the driving factors behind burrow site selection by Sungazers.

Habitat transformation within the geographic range of the Sungazer is widespread and is one of the primary threats that the species faces (Parusnath 2014). Consequently, translocation of Sungazer subpopulations from areas where developments are planned are often necessary as a mitigation to development. However, previous translocation attempts have failed (Groenewald 1992; Parusnath 2014), with a lack of knowledge of the species social structure, and the driving factors behind burrow site selection cited as some of the main reasons (Parusnath 2014). Our study attempted to address a few of the factors that may influence where Sungazers choose to construct their burrows, and therefore may guide conservation efforts by contributing to the development of translocation protocols. We recommend that natural grasslands, and habitat patches with sparse vegetation cover interspersed amongst densely vegetated areas are chosen as sites for translocations. When constructing artificial Sungazer burrows, entrances should also match the aspect of the slope, and northerly slopes and orientations are preferred. We also recommend soft-release translocation attempts on small subpopulations of Sungazers (if possible), and that careful, continuous monitoring programmes follow to identify the success rate.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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