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Habitat selection by a Threatened lizard, the Sungazer (*Smaug giganteus*): Implications for conservation

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A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa, in fulfilment of the requirements for the degree of Doctor of Philosophy.

June 2023

DECLARATION

I, Wade Stanton-Jones (Student number: 601874), declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg, South Africa. It has not been submitted before for any degree or examination at any other University.

Research protocols were cleared by the University of the Witwatersrand's Animal Ethics Screening Committee (clearance number: 2019/04/29/B) and the Human Research Ethics Committee (Non-Medical; clearance number: H19/07/37). Permits to conduct research within the Free State province of South Africa were received from the Department of Economic, Small Business Development, Tourism and Environmental Affairs (permit numbers: JM5067/2019 and 202112000008380). Permission to conduct research under Section 20 of the Animal Disease Act, 1984 (Act No. 35 of 1984) was granted by the Department of Agriculture, Forestry and Fisheries (Reference number: 12/11/1/1/20).



Wade Stanton-Jones

1st Day of June 2023

ABSTRACT

Climate change and habitat transformation are some of the primary threats that reptiles face as a consequence of persisting in their selected habitats. Some species, such as habitat specialists, may be particularly vulnerable to these threats given their restricted geographic ranges, strict habitat requirements, and limited dispersal abilities. Knowledge of the factors that drive habitat and microhabitat selection by a species, the impact that habitat transformation may have on that species, and how the species is expected to respond to climate change is necessary for informing conservation management strategies.

Smaug giganteus (the sungazer) is a threatened (Vulnerable), habitat specialist lizard that is endemic to the Highveld grasslands of South Africa. Unfortunately, suitable habitat exists in a landscape where anthropogenic activities (e.g., agriculture and mining) are prevalent, and a major threat that sungazers face is habitat transformation and fragmentation. Sungazers are unique within their family (Cordylidae) in that they rely on self-constructed burrows in specific microhabitats within the grassland matrix as long-term, often permanent, shelter and refuge sites. Because of this, aspects of their life history, and the current threats that they face, sungazers may be particularly vulnerable to the combined effects of climate change and habitat transformation. The primary aim of this thesis was to assess the consequences of habitat selection and use by sungazers by investigating the potential impact of climate change on habitat suitability for the species, the fine-scale impacts of habitat transformation, and to identify the microhabitat requirements by sungazers such that recommendations for future conservation management of the species could be made.

The potential impact of climate change on habitat suitability for sungazers was assessed by projecting their current ecological niche envelope into the future, under different climate change scenarios. The models predicted that sungazers may experience minor range contractions under the moderate case scenario, but vulnerability to climate change increased under the worst-case scenario. At the broadscale level, the models predicted that sungazers would shift their geographic range to the southwest. However, given the species life history traits, limited dispersal capacity, and the fragmented habitat in which subpopulations exist, climate tracking is unlikely, and sungazers may be more vulnerable to the effects of climate change than predicted by niche models.

An assessment of the demographics and dynamics of four sungazer subpopulations existing at sites with different habitat conditions revealed that the impact of habitat transformation on sungazers may be more devasting than what was previously reported. In this study, the sungazer subpopulations existing in habitats transformed by mining activities, and severe overgrazing have declined by more than 50% over a 16-year period. This assessment at the subpopulation level (colony level) suggests that the current size of the sungazer population is probably an overestimate.

A comparison between the microhabitat characteristics surrounding sungazer burrows and random sites in the landscape revealed that sungazers use microhabitats comprised of low vegetation cover and short grasses in which to construct their burrows. Burrow construction in these microhabitats generally occurs on northerly facing slopes. When constructing their burrows, sungazers tend to orientate burrow entrances in the same direction as the aspect of the slope but northerly directions are preferred.

This thesis provides the first insights into the potential effects that climate change may have on sungazers in the future and highlights the severity of impact that habitat transformation has on sungazers at fine spatial scales. The findings not only justify the importance of conservation management for sungazers but provide critical information to assist with future conservation protocols.

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THESIS STRUCTURE

This thesis is comprised of five chapters; a general introduction, three data chapters, and a concluding chapter. The three data chapters have been written in the format of stand-alone manuscripts to facilitate the publication process. Consequently, this has resulted in some repetition. Below are the details of each chapter:

Chapter 1: General Introduction

In this chapter, I provide the theoretical framework of the thesis and detail the aims and objectives of this research. I also introduce my study species, the sungazer (*Smaug giganteus*), and provide information on the species' ecology, distribution and habitat, and conservation status.

Chapter 2: Gazing into the future: the potential impact of climate change on habitat suitability of the Sungazer (*Smaug giganteus*)

Here, I produce a fine-tuned ecological niche model for sungazers and project the model into the future under two different climate change scenarios to assess the impact of climate change on habitat suitability for sungazers. Habitat suitability maps are refined using a natural grassland variable overlay and clipped to different extents to identify potential fine-scale changes in habitat suitability in the future. I enhance interpretation of the models through careful consideration of the species life history traits, and the anthropogenic pressures existing within sungazer distribution.

Chapter 3: Habitat transformation correlates with the decline of sungazer (*Smaug giganteus*) subpopulations

In this chapter, I provide an assessment of the population dynamics of four sungazer subpopulations that were first recorded about 16 years ago. I use four study sites, each with different habitat conditions to assess the impact that habitat transformation has had on the survival of sungazer subpopulations.

Chapter 4: Burrow site selection by the Sungazer (*Smaug giganteus*)

I investigate some of the factors that drive microhabitat selection and burrow site selection by sungazers. Such information is necessary to inform translocation protocols for this threatened species.

Chapter 5: Synthesis, limitations, recommendations for conservation, and conclusion
Finally, I contextualise the outcomes of this thesis, detail some of the limitations that were encountered and provide directions for further research on sungazers. Importantly, I use the findings of this thesis to provide recommendations for conservation management of sungazers.

PUBLICATIONS AND PRESENTATIONS

Manuscripts in review:

Chapter 3

Stanton-Jones, W.K., McIntyre, T., & Alexander, G.J. (2023). Habitat transformation correlates with the decline of sungazer (*Smaug giganteus*) subpopulations. (In review).

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Chapter 2

Stanton-Jones, W.K., & Alexander, G.J. Gazing into the future: the potential impact of climate change on habitat suitability of the Sungazer (*Smaug giganteus*). (In preparation).

Chapter 4

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Conference presentations:

Chapter 2

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CHAPTER 1

General Introduction

1.1. Theoretical Framework

1.1.1. Climate Change

Without doubt, climate change is massively impacting the world's biodiversity. Within the last five decades researchers began to reveal and acknowledge the negative effects that humans have on the global climate (Foden et al., 2019). As the human population experiences rapid growth, not only does the demand for more land occur, increasing habitat transformation and fragmentation, but there is also an increase in anthropogenic activities which accelerates the release of greenhouse gases into the atmosphere. This negatively impacts climatic patterns across the globe, and the rise of global air temperatures has also resulted in the melting of polar ice caps causing sea levels to rise (IPCC, 2021). The damage is worsened as biodiversity has already been and continues to be affected by climate change (Foden et al., 2019). In a perfect system, if species are given sufficient time, they could simply shift their distributions to track suitable conditions, they could evolve adaptations more suited to the new conditions, or they could adjust to new conditions through physiological and behavioural plasticity (Sinervo et al., 2010). While this may be the case for some species (e.g., Aragón et al., 2010), others that are unable to adjust or to track suitable conditions fast enough will likely face an increased risk of extinction (Sinervo et al., 2010). Thus, assessing how vulnerable a particular species is to climate change is important if effective conservation mechanisms are to be implemented, especially for species whose distributions are already small.

Ectothermic animals, such as reptiles, and those with geographic range edges set by climate, may have increased sensitivity to changing climatic conditions. This is because ectotherms have a strong dependence on environmental temperatures to meet physiological and ecological demands (Huey, 1991; Smith and Ballinger, 2001). Therefore, temperature is arguably one of the most important climatic factors that influences where these animals choose to seek refuge (review: Smith and Ballinger, 2001). Consequently, the probability of extinction of reptiles is increased under changing climatic conditions (Huey et al., 2009; Aragón et al., 2010), with reports of climate change having been linked to local extinctions of a few reptile species already, for example *Sceloporus* spp., *Lacerta vivipara, Liopholis*

slateri, and *L. kintorei* (Whitfield et al., 2007; Sinervo et al., 2010). Although behavioural plasticity, and even adaptation has been linked to the survival of several reptile species under changing climates (Aragón et al., 2010), the rapid rate of climate change could be detrimental to the existence of some species, and behavioural changes may not be enough of a compensation. Species relying on morphological or physiological adaptation are also at risk as evolution is a slow process that will likely be superseded by the rate of climate change (Bradshaw and Holzapfel, 2006). Thus, the most plausible solution for reptiles may be to track suitable climates, albeit a potentially temporary one when anthropogenic land use is considered.

Reptiles, in general, have specific thermal requirements which are placed under pressure with changing climatic conditions. Field-active reptiles seek to attain a target body temperature (T_{target}; *sensu* Alexander, 2007) through behavioural thermoregulation in order to maintain body temperatures (T_b) within physiological thermal optima (Alexander, 2007; Stanton-Jones et al., 2018). T_{target} is maintained through behavioural adjustments such as shuttling between sunlight and shade, and postural and orientation adjustments (McConnachie et al., 2009; Stanton-Jones et al., 2018). However, under increasing global temperatures, a possible scenario is that reptiles respond through behavioural plasticity, and T_{target} is achieved by earlier periods of activity during the day. For example, Stanton-Jones et al. (2018) suggested that because *Smaug giganteus* has a broad behavioural repertoire, individuals would respond to climate change through simple behavioural adjustments. Another study suggested that behavioural plasticity in *Chrysemys picta* could compensate for changing climatic conditions when individuals choose nesting sites (Refsnider and Janzen, 2012). Behavioural changes, however, are not without consequence; consistently higher environmental temperatures would increase hours of restriction and result in reptiles spending more time in refuge sites (e.g., shaded areas; see Taylor et al., 2020 for review) or increasing shuttling behaviours to maintain T_{target}, jeopardising foraging time, and potentially even reproduction (Sinervo et al., 2010). Several other concerns are worth noting; (1) foraging duration and frequency may be limited as the average daily temperatures increase which could compromise metabolic activities; (2) ectotherms would be at an increased risk of having their T_bs approach critical limits when active; (3) even if ectotherms were to evolve higher T_{target}s, they would simply be closer to their maximum critical thermal limits (Sinervo et al., 2010), further affecting 'normal' daily activities. Thus, under changing climatic conditions there may be behavioural

and physiological adaptations, but such adaptations are not without compromise, and in extreme cases may lead to the extinction of some species.

Predicting how species respond to climate change is complex. In some instances, population abundance of a particular species may be positively associated with rising temperatures, while in others there is a negative association (Sinervo et al., 2010; Bowler et al., 2017). Although climate change has the potential to influence the eco-physiological aspects of a species, a notable observation is that the geographic ranges of many species are beginning to shift, tracking suitable conditions (Walther et al., 2001; Konvicka et al., 2003; Freeman et al., 2018; Petford and Alexander, 2021). When climatic conditions change, reptiles with a wide behavioural repertoire may persist in their existing habitat or microhabitat (Stanton-Jones et al., 2018), and those without are likely to shift distributions to more suitable habitats or microhabitats – climate tracking – to meet their ecological and physiological demands (review: Smith and Bellinger, 2001). Though the possibility for climate tracking for the former still exists, the ability to track climatic conditions may be impacted by a species' life history traits, dispersal ability, the anthropogenic pressures (e.g., agriculture, industrial development, etc.) existing within their habitat, and geographic barriers. For example, Petford and Alexander (2021) suggested that even though *Lygodactylus incognitus*, *L. soutpansbergensis*, *Platysaurus relictus* and *Vhembelacerta rupicola* were predicted to track suitable climatic conditions under climate change, their ability to do so may be limited by their dispersal abilities, restricted geographic ranges and rupicolous life histories. Importantly, aspects of a species habitat may also be vulnerable to changing climates, for example vegetation, soil composition, food availability, etc., which could contribute to the reduction of suitable habitats. Therefore, effective conservation management requires knowledge on which factors drive species occurrence, the ecology of those species, and how they are responding to change.

1.1.2. Land Use

Undeniably, the expanding human population threatens the world's biodiversity due to its impact on the unsustainable use of land. The more the human population grows, the more the demand for land increases. Consequently, the need for more land, whether residential, industrial, or agricultural, leads to the disturbance, transformation, and even destruction of habitats. How reptiles respond to changes in their habitats is dependent on several factors: disturbance type, microhabitat availability, and the ecology and physiology of a species

(Masterson et al., 2009; Sasaki et al., 2016; Doherty et al., 2020). Consequently, habitat transformation can cause a decrease in species richness and abundances of persisting species (Santelmann et al., 2006; Masterson et al., 2009; De Solan et al., 2019).

The more that reptiles are studied, the more species are identified as being threatened with extinction. According to the IUCN Red List of Threatened species, 21% of reptiles are currently threatened with extinction (Cox et al., 2022), an increase of 2% since 2016, with many species, particularly from Africa, still not having been assessed or are data deficient (Tolley et al., 2016). In South Africa, however, there appears to be a lower extinction risk of the country's reptiles compared to the rest of the world (Tolley et al., 2019). Despite the lower extinction risk, many of the threatened species are not well protected, and the risk of extinction remains significant (Tolley et al., 2019). Habitat degradation, pollution, the introduction of alien invasive species, disease, poaching, and climate change are the some of the major reasons cited for the decline of the globe's reptile species (Gibbs et al., 2009; Masterson et al., 2009; Sinervo et al., 2010; Parusnath et al., 2017; Mingo et al., 2017). In an African context, however, agricultural expansion is the dominant cause of habitat loss and environmental disturbance (Tolley et al., 2016), and reptiles may be forced to move, modify behaviours, or evolve to persist.

The effects of habitat transformation arising from agriculture are often significant. A decline in reptile species and abundance in cultivated sites has been reported (Masterson et al., 2009) and several habitat modifications have been identified such as the removal of rocks (Webb and Shine, 1998; 2000), the use of machinery, and the destruction of certain other microhabitats, which may lead to the local extinction of certain species in particular areas. Indicator species are an example of species that could be at risk. The sungazer (*Smaug giganteus*), for example, may be regarded as an indicator species as the presence of *S. giganteus* subpopulations provides an indication that grassland remains in an ecologically sound state (Parusnath et al., 2017). Sungazers are particularly at risk from ploughing and the modification of the vegetation cover. However, because sungazer habitat falls within an agriculturally important region in South Africa (DEAT, 2005), the species is susceptible to population declines through further agricultural development. As a consequence of being an indicator species, the presence of sungazers could lead to two possible scenarios; (1) increased areas for land cultivation, and (2) increased grazing grounds. Increased cultivation is likely to be more detrimental to the indicator species but increasing the size of grazing

grounds and the density of grazers would need to be approached with caution to avoid overgrazing. Grazing can be beneficial to species living in open habitats but detrimental to those with a preference for dense vegetation (Schieltz and Rubenstein, 2016). However, if managed incorrectly, many species, including the habitat, will be negatively affected. Thus, in order to mitigate the risk of overgrazing, it is vital that livestock farmers take seasonal conditions into consideration when managing grazing livestock (Val et al., 2019).

The use of pesticides has increased significantly in agricultural practice (Aktar et al., 2009; Sarkar et al., 2021). To maximise crop production and increase food security, farmers need to protect their crops from pests, and therefore the application of pesticides is widespread. Although reptiles are not targeted through the application of pesticides, their limited dispersal capabilities could make them secondary victims of the application (Alexander et al., 2002; Gibbs et al., 2009). Physiological and behavioural implications including changes in enzymatic activity and hormonal responses, weakened body condition, increased stress, fertility impairments, development, locomotor performance, and skewed sex ratios are just some of the side effects that reptiles may experience through exposure of pesticides (DuRand et al., 2007; Amaral et al., 2012a; Amaral et al., 2012b; Bicho et al., 2013; Cardone 2015; Mingo et al., 2017). Consequently, the decline of reptile populations has been linked to the exposure of agricultural pesticides (Gibbs et al., 2009). From an ecological perspective, pesticides can disrupt the food availability for reptiles, and other organisms reliant on the resources that are controlled. Even if the effects on immediate resources are ignored, the prolonged use of pesticides can be detrimental to the existence of a species, and to ecosystems.

Habitat loss is already a concern for reptiles, but when combined with the effects of mining activities, the impact is exacerbated (Mayani-Parás et al., 2019). Mined areas cause structural changes to habitats with detrimental effects to species richness, diversity, and abundance (Altun et al., 2010; Sasaki et al., 2016). Metal pollution produced through mining practices can also have negative impacts (McIntyre and Whiting, 2012; Mayani-Parás et al., 2019). McIntyre and Whiting (2012) showed that lizards exposed to mining pollution had increased metal concentrations in blood samples. Although McIntyre and Whiting (2012) found no significant implications to body condition, the authors reported a consistent negative relationship between contaminant concentration and body condition. Poor body condition linked to metal contamination has also been reported in frogs and snakes (Sasaki et al., 2016).

It is possible that the effects are more long-term, and that in present times, prolonged exposure to mining contaminants has worsened body condition in affected species, challenging the sustainability of populations. Mine-altered environments can also skew expected sex ratios through increased metal concentrations (McIntyre and Whiting, 2012), and affect reproduction rates (Sasaki et al., 2016). Thus, to minimise the risk and damage to species, carefully designed rehabilitation and precautionary measures should be implemented. However, to maximise the effectiveness of such measures, knowing how species are affected by mining practices, and the specific habitat requirements for species is vital.

1.1.3. Habitat selection and use

Elucidating how and why animals select specific habitats is central to building knowledge around the ecology of a species. At fine spatial resolutions, knowing the types of habitats, landscapes, or landforms that animals use, and the associated limiting factors that a species experiences, is important for organismal ecology, particularly in ectothermic animals for which the environment strongly influences eco-physiological processes (Zimmerman and Tracy, 1989; Huey, 1991). While animals may be under selective pressures when choosing appropriate habitat sites, dispersal and vicariance events may also have an impact on the geographic distribution of a species and its subpopulations (Ronquist, 1997). When landscapes change because of climatic, geological, and anthropogenic processes, individuals within a population may need adapt to those changes if the populations are to persist (Parusnath, 2020). When the above changes are too rapid, the survival of a species becomes threatened.

Habitat selection and use appears to be non-random. When animals encounter a certain habitat, whether they persist depends on the associated risks and benefits of the habitat (Mayor et al., 2009). This is because of the heterogeneity of biotic and abiotic factors that exists within different habitats. These factors can influence many biological and ecological processes of an animal's life including thermoregulation (Huey et al., 1989), nesting opportunity (Kolbe and Janzen, 2002), predation avoidance (Spencer, 2002), foraging opportunity (Huey and Pianka, 1981; Whitaker and Shine, 2003), movement patterns (Eubanks et al., 2003), and population dynamics (Smith and Ballinger, 2001). Therefore, knowing which are the key indicators of a suitable habitat for a species, how individuals are selecting habitats, as well as knowing how a species functions ecologically and

physiologically within its habitat, is necessary to ensure effective implementation of conservation strategies for a species, and to ensure proper management of its habitat.

There are many factors that influence the selection and use of appropriate habitat sites. Therefore, it is important to understand the concept of limiting factors; factors that confine the distribution of a species to a particular habitat (Huey, 1991). Arguably, these factors are mostly abiotic (e.g., climate, salinity, acidity), but may also be biotic (e.g., vegetation type, prey availability, competition, predation) (Begon and Townsend, 2021). Since reptiles have a high dependence on environmental temperatures, abiotic factors (particularly climate) are generally considered the strongest limiting factors for the distributions of many species (Huey, 1991). However, while these factors place strong selective pressures on ectotherms, the amount of available habitat is equally important, and when conservation decisions are made, climate and available habitat needs to be considered in unison. While it is reasonable to assume that animals will select sites that provide for their physiological and ecological needs, at finer scales, selection pressures are likely increased in species that have small home ranges.

At finer geographic scales, species tend to select and use microhabitats that maximises alignment to their eco-physiological demands (Huey, 1991; Vitt and Caldwell, 2013). Selecting appropriate microhabitat sites can have a positive effect on behaviour, thermoregulatory efficiency, reproductive success, ability to avoid predation, foraging opportunity, and population dynamics (Huey and Pianka, 1981; Huey, 1991; Smith and Bellinger, 2001; Whitaker and Shine, 2003), all of which contribute to survival. Thus, before conservation mechanisms that involve translocations can be implemented, it is important to elucidate the factors affecting microhabitat selection and use, especially for range restricted species, and those that are sensitive to habitat heterogeneity.

Reptiles, such as lizards, will often seek refuge in burrows or crevices. These refuge sites provide a stable thermal environment, which offers protection against environmental and physiological extremes to animals that use them (Warner, 2023). There are numerous strategies that different species of lizards could employ to seek refuge or shelter in burrows. For example, lizards can use burrows constructed by other animals (e.g., Grillet et al., 2010), they may share burrows with other animals (e.g., Mulder and Keall, 2001), and some species can construct their own burrows (e.g., Van Wyk, 1992). Not only are burrows used as refuge

sites, but they may also provide foraging opportunities (e.g., Mulder and Keall, 2001). In the case of burrow sharing by two or more species, there may be advantages to both species, but there are also risks, and in such instances the reward often outweighs the risk (Mulder and Keall, 2001). For species that construct their own burrows, the potentially improved fitness consequences associated with the choice of burrow site may impose strong selection on those burrow sites. These selection pressures are probably stronger for species that use these burrows as permanent refuge sites.

Physical factors such as bare soil, vegetation type, soil quality, texture and chemistry may be strong determinants of burrow selection (Naderi et al., 2011). These factors can also influence burrow lengths and depths, which can be important for the ecology of some species (Laundre and Reynolds, 1993). Elucidating the physical factors affecting burrow preference is complex as some species may show a preference for soil type, others for vegetation, but often preference is for a combination of several factors (e.g., Song et al., 2017). However, research has also suggested that vegetation structure is another critically important factor of microhabitat selection by some species of lizards (Dias and Rocha, 2004; Attum and Eason, 2006; Masterson et al., 2008). Therefore, it is likely that vegetation structure may have an impact on which burrows are used by these lizards, or where burrows are constructed.

In addition to the ecological and evolutionary constraints associated with burrow site selection and habitat use, many animals are faced with anthropogenically driven threats such as land transformation, crop-ploughing, industrial development, and poaching (Van Wyk, 1992; McIntyre and Whiting, 2012, Parusnath et al., 2017). Anthropogenically driven threats are more influential to organisms that are habitat specialists, and therefore changes in habitat will likely alter the overall dynamics of a population (Gardner et al., 2009), along with other life history characteristics. This may be especially important when specific types of habitats are crucial for aspects of an organism's life history. Therefore, it is also vital to take ecological and evolutionary factors into consideration for conservation decision making.

Due to technological advancements, and increased accessibility to locality records of species, investigating the limiting factors of species distributions, and populations, has increased in recent times (Gaston, 2009; Foden et al., 2018; Petford and Alexander, 2021). Ecological niche models (ENMs) are now being implemented to assess species distributions, which are proving to be beneficial to conservation planning. Specifically, ENMs allow for the

identification of suitable habitats and microhabitats necessary for translocations (Steury and Murray, 2004), they can predict priority habitats that need to be conserved for species (Petford and Alexander, 2021), and more recently they have been able to predict how the distributions of species will be affected by climate change (Aragón et al., 2010; Guo et al., 2021). Therefore, the predictions made by ENMs are likely to enhance existing conservation management strategies for many species.

1.1.4. Ecological Niche Models

Geographic and environmental distributions of species have interested researchers for more than a century (Grinnell, 1917). Technological advances and increased access to species occurrence records has led to the development of ENMs which are advanced, predictive, statistical models that are used to enhance assessments of species distributions (Peterson, 2006; Peterson and Soberón, 2012; Peterson et al., 2015). Collectively, ENMs can predict suitable environmental conditions for the occurrence of a species, using a variety of techniques that could be correlative, mechanistic, or process-driven (Peterson et al., 2015). ENMs are now widely used to: 1) increase knowledge on the impacts of biological invasion (Ponti et al., 2021), 2) predict the dispersal of diseases (Peterson, 2006), 3) predict ecological and evolutionary aspects of species and their distribution (Parusnath, 2014), and of increasing importance, 4) to predict how and where species may be affected by climate change (García-Amorena, 2021; Petford and Alexander, 2021).

Before selecting the appropriate ENM, it is important to know the assumptions that underpin each model. The dimensions of a species fundamental niche can be assessed using a mechanistic model which links environmental data with a species' physiological and behavioural traits (Kearney and Porter, 2009; Peterson et al., 2015). While the model can make predictions without concern around interacting species and accessible locations, the limitation is that physiological data for many species, especially for range restricted species (Chen et al., 2018), are lacking (Peterson et al., 2015). Process-driven models follow an integrated approach using biotic interactions, niche dimensions and mechanisms such as dispersal ability to predict the occurrence of species (Dormann et al., 2012; Peterson et al., 2015). Although process-driven models are considered to produce explicit and precise predictions, they require fine resolution spatiotemporal data which are often not available (Dormann et al., 2012), or may require estimates from other models (Peterson et al., 2015).

Thus, given the specific requirements for the model, process-driven models are arguably the least used model type in ENMs.

The model type that dominates practice is the correlative model (Elith and Leathwick, 2009). Correlative models avoid describing the mechanisms of species occurrence, and instead describe the association between species occurrence and environmental data (Dormann et al., 2012). Using presence-only or presence/absence data, correlative models can predict suitable habitat and limiting factors to species distributions (Peterson et al., 2015). Even though presence/absence data may provide more accurate predictions, it is often difficult to gather absence data for species, particularly those for which data are limited. Therefore, presence-only datasets appear to be the most commonly used in correlative modelling. Despite the complexities associated with the different models, the models can be used to address different questions, and one should not be considered more superior to another (Dormann et al., 2012).

The maximum entropy (Maxent) method is a widely used tool for constructing correlative ENMs (Phillips et al., 2006; Warren and Seifert, 2011). Here, presence-only data are used to infer habitat suitability and species distributions (Phillips et al., 2006). Maxent is user friendly and can provide robust predictions for species distributions (Warren and Seifert, 2011; Merow et al., 2013; Kaky et al., 2020). However, because it is only a single model, concerns around its reliability and robustness have been raised, and ensemble approaches have been reported as offering better performance (Yackulic et al., 2013; Morales et al., 2017). Several studies have compared the predictive performance between individual models and ensemble approaches, and the results suggest that an ensemble method may not always be the superior approach (Hao et al., 2020; Kaky et al., 2020). Maxent may perform as equally as an ensemble approach but because of Maxent's ease of use and reduced computational time, it is favoured over an ensemble approach (Kaky et al., 2020). To avoid erroneous predictions and sample selection bias, it is also important that species-specific tuning (fine-tuning) is performed when designing an ENM, especially when predictions across space or time are made (Phillips et al., 2009; Anderson and Gonzalez, 2011 Merow et al., 2013). Species-specific tuning requires the testing of several models with different parameterizations to identify the model with the most robust and accurate predictions (Anderson and Gonzalez, 2011) However, species-specific tuning in ensemble methods is rare, but common in independent models. Despite the concerns around independent models, they are still known to produce accurate and robust predictions, especially when finely tuned.

1.1.5. Problem statement

The sungazer (*Smaug giganteus*) is a unique member of the Cordylidae family. Unlike other cordylids, the sungazer is a grassland specialist that has a relatively complex social structure (Parusnath, 2020); juvenile sungazers often remain in close proximity to their parents, but have also been found sharing burrows with adults that are not immediate family members (Parusnath, 2020). Sungazers seek permanent refuge in self-excavated burrows and appear to be highly philopatric lizards (Van Wyk, 1992; Stanton-Jones, 2018). This suggests there must be strong selective pressure on choosing microhabitats in which to construct burrows. Since the majority of sungazer subpopulations occur on privately-owned land in the Highveld agricultural region of South Africa, the species vulnerability to anthropogenically driven threats is greatly increased. The most recent study on the population of sungazers reported that over the last four decades, at least one third of sungazer subpopulations (as defined by the IUCN) have become locally extinct (Parusnath et al., 2017). This is primarily because of the prevalence of anthropogenically driven activities, habitat fragmentation, and the illicit pet trade occurring in their geographic range. However, it is important to note that the assessment by Parusnath et al. (2017) was at a broadscale level, i.e., the number of subpopulations. How these threats are impacting the species at finer geographic scales (within subpopulations) remains largely unknown.

To assist with the conservation of the species, Parusnath (2014) and Parusnath (2020), developed ENMs to identify areas of suitable habitat for sungazers. The models predicted vegetation type, soil, geology, isothermality, seasonal precipitation, temperature, and annual temperature range to be important variables for the occurrence of sungazers (Parusnath, 2014; Parusnath, 2020). These predictions provided insight into where sungazers occur and formed the basis for future predictions of suitable habitat for the species. Since climate change is of growing concern for many species, how sungazers will respond to it remains unknown, but requires a finely tuned model with cognisance to the species life history and physiological traits to make accurate predictions. It is likely that the combined effects of climate change and habitat transformation within their geographic range will increase their risk of extinction. Thus, how the species is expected to respond to climate change is necessary for future conservation management of the species.

Despite attempts to translocate sungazers from land that was earmarked for development to new locations, these attempts appear to have been unsuccessful (Groenewald, 1992;

Parusnath, 2014). For example, a subpopulation of sungazers was translocated to the Golden Gate Highlands National Park, and burrow occupancy rates were as low as 10% less than 50 days after translocation occurred (Groenewald, 1992). Although the poor success rate was argued to be a result of predation, it is possible that it could have been a result of unsuitable artificial burrows, especially considering that translocated individuals did not seem to use these burrows (Groenewald, 1992). Parusnath (2020) reported a personal communication with Groenewald that a survival rate of less than 2% over the two years following translocation was estimated. However, no formal studies have been conducted to confirm this. For effective translocations and reintroductions of individuals and subpopulations, the factors that drive microhabitat selection, and influence where the lizards choose to construct their burrows, needs to be better assessed so that the receiving sites are suitable for the translocated individuals. These factors also need to be used in conjunction with expected suitable habitat for the species under climate change.

1.1.6. Aims and objectives

Smaug giganteus is a habitat specialist that has evolved to live within a grassland habitat. However, the species is currently threatened by anthropogenic activities (e.g., mining and agricultural practice leading to habitat transformation) occurring within its geographic range. Thus, even though sungazers have evolved within the grassland habitat, they are now experiencing the consequences of living within that habitat. The primary aim of this thesis was to investigate the consequences of habitat selection and use by *S. giganteus*. Firstly, the effects of climate change on habitat suitability for sungazers were assessed to evaluate how the species could respond to changing environmental conditions. Secondly, the demographics of sungazer subpopulations over a 16-year period across four different study sites were assessed, and the population trends were related to site history and characteristics. The last main component in this thesis analysed the factors that may constrain burrow site selection in the species to identify important microhabitat correlates that would inform future conservation strategies. Overall, this thesis provided insights into: a) how vulnerable sungazers are to climate change, b) the fine-scale impact of habitat transformation on sungazer subpopulations, c) how sungazers select sites for burrow construction, and d) conservation management strategies. Specific aims and objectives are detailed below:

1) **Assess the potential impact of climate change on habitat suitability for *Smaug giganteus* (Chapter 2):** I tested the hypothesis that sungazers would be vulnerable to the effects of climate change.
    a. Produce a fine-tuned ENM for *S. giganteus.*
    b. Project the ENM into the future, at 20-year intervals up to 2100, under two climate change scenarios.
    c. Relate life history traits, and anthropogenic pressures to the model predictions to enhance interpretation.

2) **Assess the impact of habitat transformation on subpopulations of *S. giganteus* over a 16-year period (Chapter 3):** Using subpopulation records from McIntyre (2006), I tested the hypothesis that the survival of sungazers will be highest in overgrazed habitats.
    a. Quantify the recapture rates across four study sites: two mining, one overgrazed, and one undisturbed.
    b. Assess burrow fidelity using recaptured individuals.
    c. Estimate site-specific subpopulation change over the period, and across the four study sites.
    d. Measure dispersal distances of sungazers across the different study sites.
    e. Quantify and compare changes in sex ratio of sungazers across the different study sites, and over the 16-year period.

3) **Assess the microhabitat characteristics that may be influencing burrows site selection by *S. giganteus* (Chapter 4):** I tested the hypothesis that sungazers select microhabitat associated with low vegetation cover and short grass height in which to construct their burrows.
    a. Estimate the percentage vegetation cover within a 4 m^2 quadrat centred on sungazer burrows and compare against random sites.
    b. Measure the mean grass vegetation height within the quadrat and compare those against random sites.
    c. Quantify and compare the abundance of animal faeces within the quadrat on sungazer burrows and random sites.
    d. Quantify trends in burrow orientation and slope aspect.

4) **Conservation recommendations for *S. giganteus* (Chapter 5):**
   In this chapter, I synthesise the findings in this thesis to provide recommendations for conservation management of *S. giganteus*. Specifically, I provide recommendations to enhance translocation protocols for the species.

1.2. Study species

1.2.1. Introduction to the species

The sungazer (*Smaug giganteus*), also known as the giant dragon lizard, is a heavily armoured lizard belonging to the Cordylidae family, a family of lizards that is endemic to sub-Saharan Africa (Branch, 1998). *Smaug giganteus* is the largest of all the Cordylidae species, commonly reaching total lengths of 400 mm (Van Wyk, 1992). Individuals from the eastern side of the population tend to be larger than those from the west (Parusnath, 2020). Sungazers have enlarged, keeled caudal spines and a pair of prominent, elongated occipital spines which makes them easily distinguishable from the other members within their family (Van Wyk, 1988). As their common name suggests, sungazers often bask in an anterior body-up posture seeming as if they are gazing at the sun (Fig. 1.1; Van Wyk, 1992; Branch, 1998). However, recent research suggests that sungazers spend more time basking in an orientation that exposes their dorsal surfaces to the sun, with the purpose of increasing the rate of heat gain (Stanton-Jones et al., 2018).



Figure 1.1. An adult sungazer (*Smaug giganteus*) basking in a typical anterior body-up posture.

Sungazers are diurnal, ambush-foraging lizards that live in self-constructed burrows (Fig. 1.2) in which they spend most of their lives. Activity occurs mainly near burrow entrances and

movements are rarely more than 2 m from burrow entrances, unless the lizards are mate searching or for occasional foraging forays (Van Wyk, 1992; Ruddock, 2000; Stanton-Jones, 2018). Since sungazers are ambush-foragers, when they are active outside of their burrows they will opportunistically forage on a range of invertebrates, particularly on species belonging to the Coleoptera, Diplopoda, Orthoptera, Hymenoptera, Hemiptera and Lepidoptera (Jacobsen, 1989; Van Wyk, 2000). They are more active in spring, summer, and autumn (September-April), and generally brumate during the winter season (May-July; Van Wyk, 1992), with occasional brief emergences from their burrows (Stanton-Jones, 2018). Reproduction is dependent on the availability of resources, and females may only breed every two or three years, giving live birth to not more than three individuals in a litter (Van Wyk, 1992). The growth rate of sungazers is relatively slow; individuals may take up to five years to reach sexual maturity (snout-vent length ~165 mm; Van Wyk, 1992). The low reproduction rate, fecundity, and long lifespan (>20 years) indicates that *S. giganteus* has a K-selection life history strategy (Van Wyk, 1992).



Figure 1.2. A self-constructed sungazer (*Smaug giganteus*) burrow, easily identifiable by the oval-shaped entrance and bare soil patch leading to the entrance.

1.2.2. Distribution and habitat

Smaug giganteus is endemic to the Highveld grasslands of South Africa, with subpopulations restricted to the northern Free State and southwestern parts of Mpumalanga provinces. The geographic range is restricted to elevations between 1400-1800 masl, and in general, is characterised by hot summers with widespread rainstorms (November-March) and cold and dry winters (June-August) with frequent frost spells at night (Van Wyk, 1992). Although *S. giganteus* has previously been listed as occurring in Kwa-Zulu Natal (Bourquin, 1993;

Bourquin, 2004), evidence based on a survey in conjunction with an ecological niche model suggests that these records did not represent an indigenous subpopulation (Armstrong, 2011). Currently, the Free State and Mpumalanga provinces are the only provinces where natural subpopulations of the species are known to occur.

Sungazers can often be found in short grass patches within the *Themeda trianda* grassland matrix (Fig. 1.3; Bates et al., 2014; Parusnath, 2014). It is likely that because short grass patches tend to be rare, the availability of these microhabitats could be a limiting factor to the establishment of sungazer aggregations. Sungazer burrows are easily identifiable by their oval-shaped entrances, a mid-ridge along the floor, and a smooth bare soil patch leading outside the burrows (Fig. 1.2; Van Wyk, 1992). Typically, burrows range between 530 mm and 3820 mm in length and frequently descend more than 400 mm below the surface (Jacobsen et al., 1990; Van Wyk, 1992). A mean burrow density of 6.14 ± 0.89 burrows/ha has been reported (Parusnath et al., 2017) but burrow densities may range between 1-16 burrows/ha with lower densities (< 6 burrows/ha) being more common (Parusnath et al., 2017). Most burrows are occupied by a single individual (mean: 1.83 sungazers/burrow; Parusnath et al., 2017), but juveniles and sub-adults do co-habit with adults, usually with either a maternal or paternal parent or full sibling (Parusnath, 2020). Occasionally, multiple adults can be found sharing a single burrow, usually with immediate family members (Parusnath, 2020). Because several individuals may co-habit a single burrow, and that relatedness between individuals within colonies is high, there is obvious complexity of sociality and population structure in the species (Parusnath, 2020).



Figure 1.3. *Smaug giganteus* grassland habitat. Sungazers are generally found within short grass patches amongst gently sloping *Themeda trianda* grasses.

1.2.3. Conservation status

Smaug giganteus was originally listed as 'Vulnerable' (McLachlan, 1978) and has retained this threat status ever since (Bates et al., 2014; Tolley et al., 2019). Due to the prevalence of anthropogenically driven activities in its range, and because the species occurs within a restricted geographic range, it is not surprising that the species is listed as threatened (Van Wyk, 1992; Ruddock, 2000; Parusnath et al., 2017). It is evident that *S. giganteus* deserves its threatened status as a recent study on the population status of the species reported a significant decline in the number of subpopulations compared to historical numbers (Parusnath et al., 2017). However, at finer spatial scales, it is likely that the population decline is even more dramatic as subpopulations still persisting may also have decreased in size. This is because many subpopulations are exposed to anthropogenic pressures such as mining, habitat transformation and fragmentation, and the illegal pet trade (McIntyre and Whiting, 2012; Parusnath et al., 2017). Parusnath et al. (2017) reported that, on average, at least 40 individuals were being exported under permit from South Africa annually, and since evidence of captive breeding for the species did not exist, individuals were presumed to have been wild caught, and simply laundered as captive bred individuals. Such anthropogenically driven activities have the potential to affect the population structure and ecology of the species. Therefore, knowing the threats and the severity of the threats to which sungazers are exposed, how these lizards interact with their environment, and the ecological drivers of burrow site selection, is crucial for future conservation efforts.

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CHAPTER 2

Gazing into the future: the potential impact of climate change on habitat suitability of the Sungazer (*Smaug giganteus*)

ABSTRACT

Climate is arguably one of the most influential factors determining the geographic range of reptile species. Consequently, climate change is expected to be detrimental to many reptile species and has resulted in some shifting their distributions to track suitable conditions. For habitat specialists such as the sungazer (*Smaug giganteus*), the ability to track suitable conditions may be limited by their life history traits, and the amount of available suitable habitat, and these species may therefore face an increased risk of extinction. I assessed how climate change could potentially impact the geographic range of the sungazer, a grassland specialist which is currently listed as Vulnerable. I modelled the current distribution of sungazers using bioclimatic and environmental variables to estimate its ecological niche envelope. I then projected the ecological niche envelope to 2040, 2060, 2080 and 2100 under two climate change scenarios using Shared Socioeconomic Pathways (SSP), SSP245 (moderate case) and SSP585 (worst-case). A mean ensemble of three global circulation models for each time period and climate change scenario was then used to create habitat suitability maps which were refined using a natural grassland variable overlay. Resulting maps were clipped to the current extent of occurrence (EOO) and interpreted distribution to identify potential fine-scale changes in habitat suitability. Models predicted that habitat suitability for sungazers will remain stable under SSP245, with a 3% decline in habitat suitability within the interpreted distribution by 2100. However, models predicted a 24% decline in habitat suitability under SSP585. At a broader scale (buffered EOO), I found that habitat suitability increased in south-western regions, which was also more prominent under SSP585. Although this finding suggests that sungazers could potentially track favourable conditions, their life history and low dispersal ability makes climate tracking unlikely. Because sungazers occur within an agriculturally dominated region of South Africa, further land use developments are likely to affect the survival of the species. Thus, careful conservation management is essential for the species. This study has shown that modelling future distributions of species may identify potential changes, but predictions should be interpreted with caution.

Keywords: climate change, ecological niche model, habitat specialist, habitat suitability

2.1. Introduction

The expansion of the human population, and associated anthropogenic activities, in recent decades has caused greenhouse gases to rise significantly (IPCC, 2022). Consequently, the effects of climate change on global biodiversity are exacerbated. Since climate is an important factor that influences organismal biology, it is not surprising that the effects of climate change have imposed challenges to the survival of many species (Parmesan, 2006; Sinervo et al., 2010). Some species, such as many reptiles, whose life history traits and geographic ranges are highly dependent on climate (Moreno-Rueda et al., 2011, Böhm et al., 2016, Perold et al., 2021), may be more vulnerable to climate change than others (Parmesan, 2006). More than 80% of reptile species are predicted to be highly sensitive to climate change, and nearly half may not be able to adapt to changing conditions effectively (Böhm et al., 2016). Predictions indicate the extirpation of nearly 40% of lizard populations, and the extinction of approximately 20% of lizard species (Sinervo et al., 2010). These predictions highlight the importance of climate change mitigation measures, as species that are unable to respond to climate change fast enough will likely face an increased risk of extinction.

Responding to climate change may be complex, and some reptile species may respond through behavioral or physiological plasticity (Sinervo et al., 2010). However, changes in behaviour to meet thermal demands may have eco-physiological consequences. For example, reduced surface activity to avoid critical thermal limits may still be sufficient for a species to achieve its thermal optima, but could constrain foraging time, aspects of reproduction, and could limit growth rates (Sinervo et al., 2010). Although some reptile species may eventually evolve to tolerate higher environmental temperatures, the consequence of evolving this trait may have a negative impact on other life history traits which are thermally dependent (e.g., reproduction). Evolving a tolerance for a different thermal environment would also require a large temporal scale for genetic variation to be effective (Bradshaw and Holzapfel, 2006). For many reptile species, however, climate change may be too rapid for evolution and adaptation to occur, and these species may not be able to persist under rapidly changing climates.

Climate may arguably be one of the most influential factors that determines the geographic range of reptiles. Thus, a more likely response to climate change is for reptiles to shift their geographic ranges to track suitable conditions (Bradshaw and Holzapfel, 2006). In a perfect system, reptiles would simply track suitable conditions, and eco-physiological processes could function as they are. However, not only may physical barriers, such as mountains or

water bodies, limit dispersal into future climatically suitable areas, but these areas may also be compromised by habitat loss and fragmentation because of anthropogenic land use (Brook et al., 2008; Garcia et al., 2014; Gouveia et al., 2016; Albaladejo-Robles et al., 2023). Species biological traits may also hinder their ability to track suitable conditions (Bradshaw and Holzapfel, 2006; Böhm et al., 2016). This is particularly true for habitat specialists, species with low dispersal rates, and species with restricted geographic ranges (Parmesan, 2006; Böhm et al., 2016; Petford and Alexander, 2021). In such cases, this may cause geographic range contraction under future climates (Parmesan, 2006; Petford and Alexander, 2021). Nevertheless, knowing how the geographic distribution of a species could change in future climates provides valuable information for identifying conservation hotspots, particularly for high-risk species.

The sungazer (*Smaug giganteus*) is a threatened (Vulnerable; IUCN, 2022) habitat specialist lizard endemic to the Highveld grasslands of South Africa. Its geographic range is restricted to the northern Free State and southernmost parts of the Mpumalanga provinces (De Waal, 1978; Jacobson, 1989; Parusnath et al., 2017). These regions are heavily impacted by agricultural activity (DEAT, 2005), and as a result, approximately only half of sungazer natural habitat remains in a natural state (Parusnath et al., 2017). Even though the rate of natural grassland decline has slowed significantly in recent decades (Parusnath et al., 2017), the species is still be exposed to other anthropogenic pressures such as poaching and land use for mining (e.g., McIntyre, 2006). These pressures, along with an already small and restricted geographic range are likely to increase the sungazer's vulnerability to climate change.

Sungazer life history does not appear to be conducive to responding to changing climates. Sungazers are large-bodied, long-lived ambush foragers, that can spend their entire life seeking refuge in a single self-constructed burrow (Van Wyk, 1992; Bates et al., 2014; Parusnath, 2014). Because of this, sungazers have strict habitat requirements at both the macro and micro scale, and changes in their environment are expected to be detrimental to the long-term survival of the species. Sungazers are mostly active within a 2 m radius of their burrow entrances and dispersal is limited (Van Wyk, 1992; Stanton-Jones, 2018). Since litter size is relatively small (maximum of three young per litter), and live birth may be biennial, reproductive rate in sungazers is low (Van Wyk, 1992). This not only reduces the chances of adaptation to climate change through evolutionary mechanisms but also limits dispersal into suitable habitats in future climates. Even though the life history traits of sungazers may

increase the species risk of extinction under climate change, knowing potential changes of their geographic distribution in future climates is vital for conservation planning.

In this study, I used two climate change scenarios under the Coupled Model Intercomparison Project Phase 6 (CMIP6) and assessed the potential impact that each scenario would have on the geographic range of *S. giganteus*. Although Stanton-Jones et al. (2018) predicted that sungazers could adjust to climate change through behavioural adjustment, the species life history traits, relatively low target body temperature, and the anthropogenic pressures to which subpopulations are exposed, increases their vulnerability to climate change, and the species may be more at risk of extinction than previously assessed. Because the moderate case climate change scenario assumes that conditions do not deviate significantly from current climate, I predicted that in the near future, the current geographic range of sungazers would remain stable, but that changes would become apparent in distant futures. I also tested the hypothesis that the worst-case climate change scenario would result in a substantial contraction of the species current suitable habitat, particularly in distant futures.

2.2. Methods

2.2.1. Sungazer occurrence records

Presence-only records of *Smaug giganteus* were gathered from my own field work (2015 to 2022), Parusnath (2014), Parusnath (2020), and from the Endangered Wildlife Trust. The resulting combined dataset included 1 957 locality records. Given that sungazers are restricted to a relatively small geographic range (Parusnath et al., 2017), and because the dataset used in this study was large, it is possible for spatial sampling bias to exist when constructing and running an ecological niche model (ENM). Thus, to minimize any potential effects of spatial autocorrelation, the dataset was cleaned, and spatially filtered with a 5 km radius using the *spThin* package (Aiello-Lammens et al., 2015) in *R* 4.1.1 (R Core Team, 2021). The number of locality records was reduced to 171.

2.2.2. Environmental variables

Bioclimatic variables for current and future conditions were downloaded from the WorldClim database (Version 2.1; www.worldclim.org; Fick and Hijmans, 2017). For current conditions, I used the standard 19 bioclimatic variables at a resolution of 30 arc-seconds (arcsec; ~1 km). Because sungazers construct their own burrows which are often used as permanent refuge sites (Van Vyk, 1992), I also included soil composition (% sand, % silt, and % clay) and the

cation exchange capacity (CEC) of soils (Batjes, 2004) when constructing the ENMs. Geology (scale = 1: 1 000 000; Council for Geosciences, 2018); and elevation (30 arcsec resolution; Fick and Hijmans, 2017) were also downloaded and included as predictor variables in the models. Vegetation type was excluded as a variable since it is likely that patterns of vegetation type will also change with changing climate. All bioclimatic and environmental variables were cropped to a rectangular shaped buffer (buffered extent) in QGIS (Version 3.26.0), with a perimeter delimited to within a half a degree square outside of the minimum convex hull (Extent of Occurrence; EOO) for sungazers (Fig. 2.1). I tested for correlations among the 19 bioclimatic variables using a Pearson's correlation coefficient in *R* 4.1.1 (R Core Team, 2021). Careful consideration was made to highly correlated ($|r| \geq 0.75$) variable pairs, and the variables considered to be the most ecologically important for sungazer distribution were included in the ENM for sungazers (Table 2.1).



Figure 2.1: Map of South Africa showing the different scales used to predict habitat suitability for sungazers. Dark grey represents the rectangular buffer zone (142 884 km^2) from which current and future sungazer distributions were modelled. Inside the buffer zone is the EOO (black; 40 573 km^2) and the interpreted distribution (light grey; (21 985 km^2)) for sungazers.

Table 2.1: Bioclimatic and environmental variables that were retained after highly correlated variable pairs were inspected and variables removed accordingly. The variables listed below were used to construct the sungazer species distribution model.

Code	Description	Reference
Bio 1	Annual mean temperature	
Bio 3	Isothermality	
Bio 6	Minimum temperature of the coldest month	Fick and Hijmans, 2017
Bio 12	Annual precipitation	
Bio 15	Precipitation seasonality	
Bio 17	Precipitation of the coldest quarter	
soilcec	Cation exchange capacity of soils	
clayperc	Percentage of clay content in soils	Batjes, 2004
sandperc	Percentage of sand content in soils	
siltperc	Percentage of silt content in soils	
elevation	Elevation	Fick and Hijmans, 2017
sggeol	Geology	Council for Geosciences, 2018

For projections into the future, I used two Shared Socioeconomic Pathways (SSPs) under the Coupled Model Intercomparison Project Phase 6 (CMIP6); SSP245 (moderate case) and SSP585 (worst-case). These two scenarios offer different realistic predictions for future climate based on socioeconomic and technological trends. The SSP245 scenario ('middle of the road'; Riahi et al., 2017) predicts that trends in socioeconomic and technological sectors, as well as carbon dioxide emissions, do not deviate significantly from current conditions. By contrast, the worst-case scenario, SSP585 ('Taking the Highway'; Riahi et al., 2017), predicts very little mitigation measures for climate change, and a fossil-fuel dominant future.

GCMeval (gcmeval.met.no) was used to identify models that perform relatively well over southern Africa. Following this, three global circulation models (GCMs) were selected to create an ensemble for projections up to 2100: 1) First Institute of Oceanography Earth System Model version 2.0 (FIO-ESM-2-0); 2) Max Planck Institute for Meteorology Earth System Model using the high-resolution protocol (MPI-ESM1-2-HR); and 3) Meteorological Research Institute Earth System Model version 2.0 (MRI-ESM2-0). Using GCMeval, the ensemble for the selected models was inspected to ensure that the models were normally

distributed. Bioclimatic variables for each GCM and SSP scenario were downloaded, and only the relevant bioclimatic variables identified for current conditions (Table 2.1) were processed for modelling into near (2021–2040), medium (2041–2060 and 2061–2080), and distant (2081–2100) futures.

2.2.3. Ecological niche model

Sungazer distribution models were constructed following the maximum entropy (Maxent) approach. Maxent has a proven track record for dealing with presence-only records when modelling species distributions (Elith et al., 2006; Phillips et al., 2006). However, species-specific tuning when using Maxent is necessary for optimal predictive power, and results in models that perform as efficiently to other ensemble approaches (Hao et al., 2020; Kaky et al., 2020, Valavi et al., 2022).

To maximize the predictive ability, 4 187 occurrence records of all reptiles (SANBI, 2022) within the buffered extent were used to create a bias file for background point sampling. The bias file was created in *R* 4.1.1 (R Core Team, 2021) and was used to randomly sample 10 000 background points through different model iterations. The *R* package, ENMeval 2.0 (Kass et al., 2021), was used to construct a variety of models with different levels of complexity. To construct these models, I implemented the Maxnet algorithm (Version 0.1.4) which employs an infinitely weighted logistic regression to fit Maxent models (Phillips et al., 2017; Phillips, 2021). The algorithm places strong emphasis on background points compared to presence points and uses the same feature classes (FC: linear (L), quadratic (Q), hinge (H), product (P) and threshold (T)), and regularization multipliers (RM) as the traditional *Maxent.jar* algorithm (Phillips et al., 2017). Thus, I constructed models with varying combinations of FCs (L; LQ; H; LQH; LQH; LQHP; LQHPT), and RMs (0.5–4.5, increments of 0.5).

Because this study investigated cross-time projections, the spatial block method (a variant of *k*-fold cross-validation) was used for data partitioning (Muscarella et al., 2014). Here, occurrence and background data are partitioned equally into four bins based on longitude and latitude; one testing bin and three training bins (Muscarella et al., 2014). The above resulted in 54 model runs, each with a different combination of FCs and RMs. The model with the lowest delta Akaike Information Criterion corrected for small sample sizes (AIC_c) was considered to provide the optimal settings for generating the sungazer ENM (Warren and

Seifert, 2011). However, to ensure that this model prevented overfitting, the threshold-independent metric (area under the curve; AUC), the 10th-percentile omission rate (OR_{10}) and the minimum training presence omission rate (OR_{mtp}) were also inspected (Anderson and Gonzalez, 2011). These model settings were used to predict the current distribution of sungazers. The model was then projected into the near, medium, and distant futures using the three different GCMs under SSP245 and SPP585 scenarios, resulting in 24 model runs across different temporal scales and scenarios.

2.2.4. Habitat suitability assessment

Models from the three GCMs under the SSP245 and SSP585 scenarios were combined to create a simple mean ensemble for each scenario and time period (Palm and Zellner, 1992; Petford and Alexander, 2021). To assess habitat suitability, the predicted distribution maps from the ensembles and current conditions were converted into binary maps (suitable/unsuitable habitat) with the 10th-percentile training presence value used as the threshold for conversion (Liu et al., 2005). Because sungazers occur in natural grassland within their distribution (Parusnath et al., 2017), I used the most recent land cover map of South Africa (DFFE, 2020) to extract this land cover type, resulting in a binary land cover map distinguishing natural grasslands from the other land cover types. Since no future land cover types exist for my study region, and because Parusnath et al. (2017) reported stability amongst natural grassland, I overlayed the binary natural grassland layer onto my binary maps for current and future distributions of sungazers. This additive approach resulted in maps with values ranging from zero to two, with two representing areas of suitable habitat that consists only of natural grassland. The resulting maps were then used to create binary habitat suitability maps that provide a more realistic representation of sungazer distribution. These maps were then clipped to the EOO and interpreted distribution for *S. giganteus*.

The GRASS *r.report* function in QGIS (Version 3.26.0) was used to calculate the predicted area of suitable habitat for current and future climate scenarios under the three scales (buffered extent, EOO, interpreted distribution). For an estimate of how much area is considered suitable for sungazers, area measures were calculated as a percentage of the area of each resolution. This was also done for all future predictions. The percentage of habitat change (+/–) between current conditions and future conditions was also calculated, and Schoener's D statistic from the *nicheOverlap* function of the *dismo* package (Hijmans et al.,

2017) in *R* 4.1.1 (R Core Team, 2021) was used to quantify niche overlap between current and future predictions.

2.3. Results

2.3.1. Sungazer ENM

The sungazer distribution model showed no obvious signs of overfitting and performed well under the tuning parameters (Table 2.2). The average test AUC was 0.905 ± 0.022, indicating very good model performance (Swets, 1988). Habitat conditions appear to be more suitable for sungazers at higher elevation (> 1500 m.a.s.l.) and under increasing values of annual mean temperature (Bio 1), minimum temperature of the coldest month (Bio 6), annual precipitation (Bio 12), and precipitation seasonality (Bio15; Fig. 2.2). Conversely, when isothermality (Bio 3) and precipitation of the coldest quarter (Bio 17) increases, habitat conditions become less suitable for the species (Fig. 2.2). At the soil level, higher percentages of clay and sand content increases the probability of occurrence of sungazers, but for soils composed of more than 25% silt had reduced habitat suitability (Fig. 2.2). Soils with a cation exchange capacity (CEC) of 15-25 meq/100g appear to result in an increased probability of sungazer occurrence. Most geology types were considered suitable for sungazers (Fig. 2.2).

Table 2.2. Tuning parameters and evaluation metrics for the optimum sungazer ENM. The feature classes (FC), regularisation multiplier (RM), Akaike information criterion corrected for small sample sizes (AIC_c), area under the curve (AUC), 10^{th}-percentile omission rate (OR_{10}), and the minimum training presence value (OR_{mtp}) are presented.

Species	**FC**	**RM**	**Δ AIC_c**	**AUC_{test}**	**OR_{10}**	**OR_{mtp}**
Smaug giganteus	LQHP	1.5	0.00	0.905	0.14	0.02

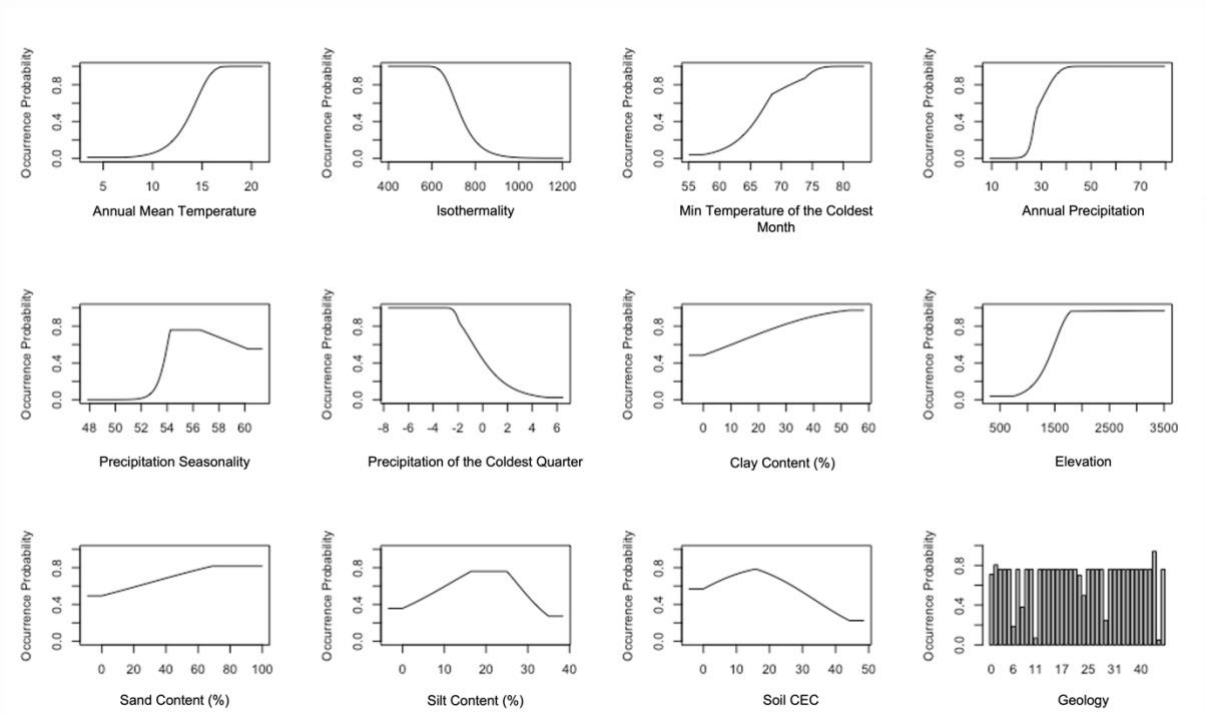


Figure 2.2. Response curves of the bioclimatic and environmental variables for the sungazer ENM. The x-axis of each graph represents each variable, and the y-axis indicates the probability of occurrence (cloglog output) for sungazers. The Geology plot is indicative of the different geology types (categorical data).

2.3.2. Current predictions

The proportion of suitable habitat varied depending on the scale. At the broadscale level (buffered extent), approximately 25 000 km^2 was predicted suitable for sungazers under current climatic conditions, accounting for 18% of the total area of the buffered extent (Table 2.3). At smaller scales, the EOO and interpreted distribution, the areas of suitable habitat predicted for sungazers were approximately 19 400 km^2 and 10 200 km^2, respectively. Although both these measures were proportionally more than the measure at the scale of the buffered extent, they are still relatively low considering that proportion of suitable habitat at these finer scales was less than 50% (Fig. 2.3.; Table 2.3).

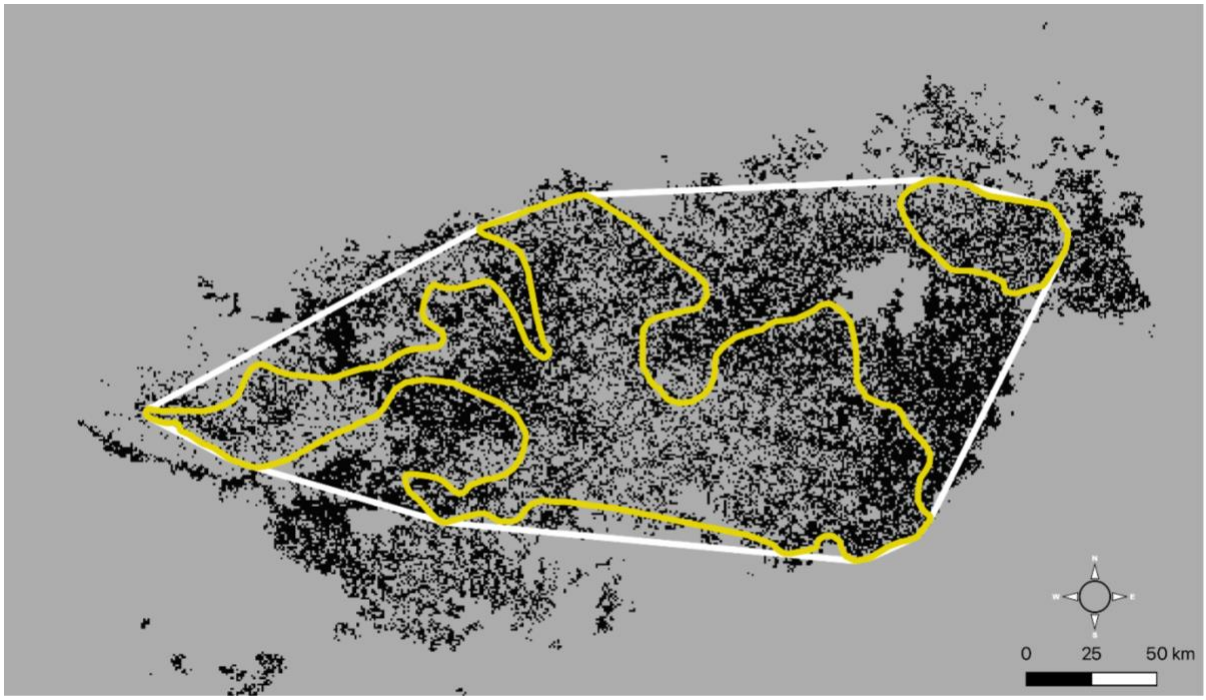


Figure 2.3: Predicted binary habitat suitability map for sungazers under current conditions. The binary (suitable/unsuitable) map shows the buffered extent overlayed with the current EOO (white boundary) and interpreted distribution (yellow boundary) for sungazers. The 10th-percentile training presence value was used as a threshold for conversion to binary format. Black = suitable. Grey = unsuitable.

2.3.3. Future predictions

Predicted suitable habitat for sungazers differed under the two climatic scenarios, with SSP245 showing minor differences compared to current predictions, and SSP585 showing more prominent differences. Differences in predicted suitable habitat also occurred within the different scales in each of the climatic scenarios (Table 2.3).

2.3.3.1. Interpreted distribution

In the near- and medium-term futures, and under moderate climatic conditions (SSP245), the proportion of suitable habitat within the interpreted distribution of sungazers was similar to the prediction for current conditions (46%; approximately 10 200 km^2), and niche overlap was also high in these periods (Table 2.3). However, an eastward shrinking trend in habitat suitability was observed in distant futures under SSP245 (Fig. 2.4b). Approximately 9 900 km^2 (a decrease of 3% from current conditions) of suitable habitat was predicted to remain by 2100 under moderate conditions (Table 2.3). By comparison, decreasing trends in habitat suitability were more noticeable under SSP585 (Fig. 2.4c). Suitable habitat was predicted to

decrease marginally (3%) in near- and medium-term futures, a similar trend to distant futures under SSP245. In distant futures, however, suitable habitat within the interpreted distribution for sungazers decreased substantially (24%) under SSP585, with only 7 700 km^2 of suitable habitat predicted to remain by 2100 (Table 2.3). Loss of suitable habitat predominantly occurred from the east and west edges of current sungazer distribution, with the shrinking trends more prominent compared to the SSP245 scenario (Fig. 2.4). Niche overlap was also lower by 2100 under SSP585.

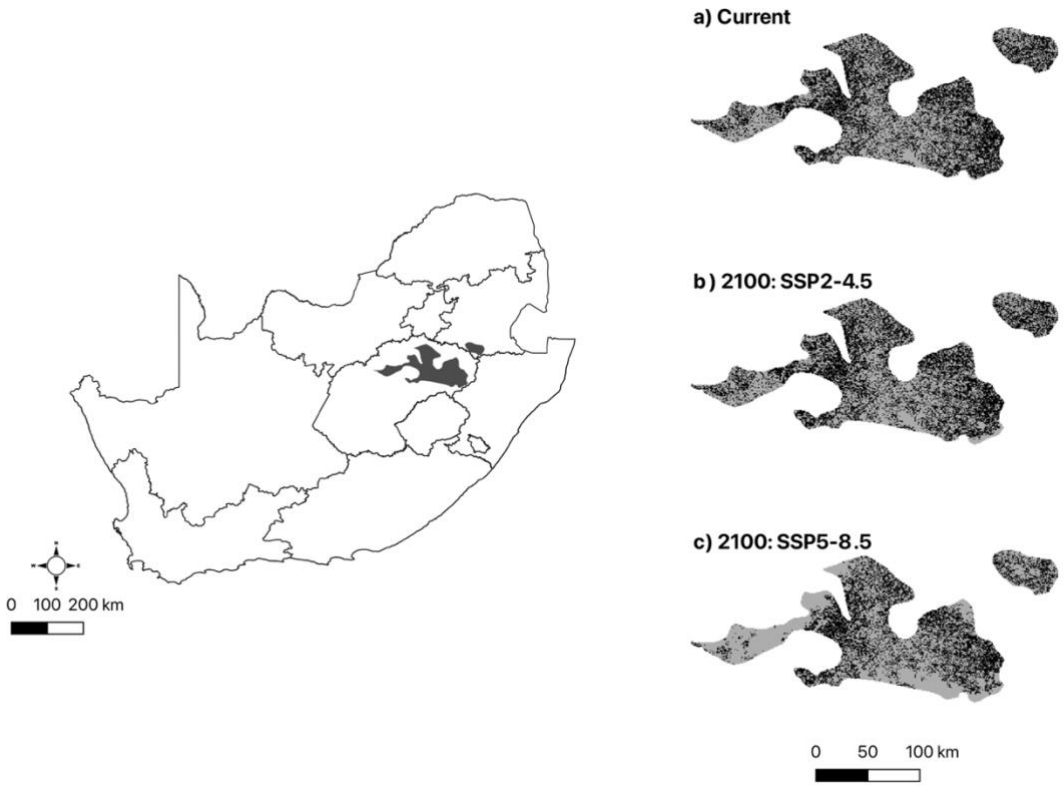


Figure 2.4: Habitat suitability maps showing the predicted distribution of sungazers within their current interpreted distribution. Maps shown represent current (a), and future 2100 (moderate case, SSP2-4.5 (b) and worst-case, SSP5-8.5 (c)) predictions. The suitability maps are binary, showing regions which are suitable (black) and unsuitable (grey). SSP = Shared Socioeconomic Pathways.

2.3.3.2. Extent of occurrence

At the scale of the EOO of sungazers, habitat suitability was predicted to marginally increase (2%) under SSP245 in near- and medium-term futures (Table 2.3). Although habitat suitability during these periods partially reduced around the east and west edges of the EOO, suitable habitat began to shift south-westerly (Fig. 2.5b). In distant futures under SSP245,

habitat suitability is predicted to decrease by 4% from current predictions by 2100 but niche overlap with current predictions remained high (Table 2.3). Conversely, under the SSP585 scenario, suitable habitat within sungazer EOO shrank more rapidly compared to SSP245 (Fig. 2.5), with approximately 12 500 km^2 (down 35% from current predictions) predicted to remain by 2100. Niche overlap in distant futures was also lower than in near- and medium-term futures (Table 2.3). Under SSP585, prominent declines in east, west, and north-east edges of the EOO were observed with central and south-westerly regions remaining suitable (Fig. 2.5c).

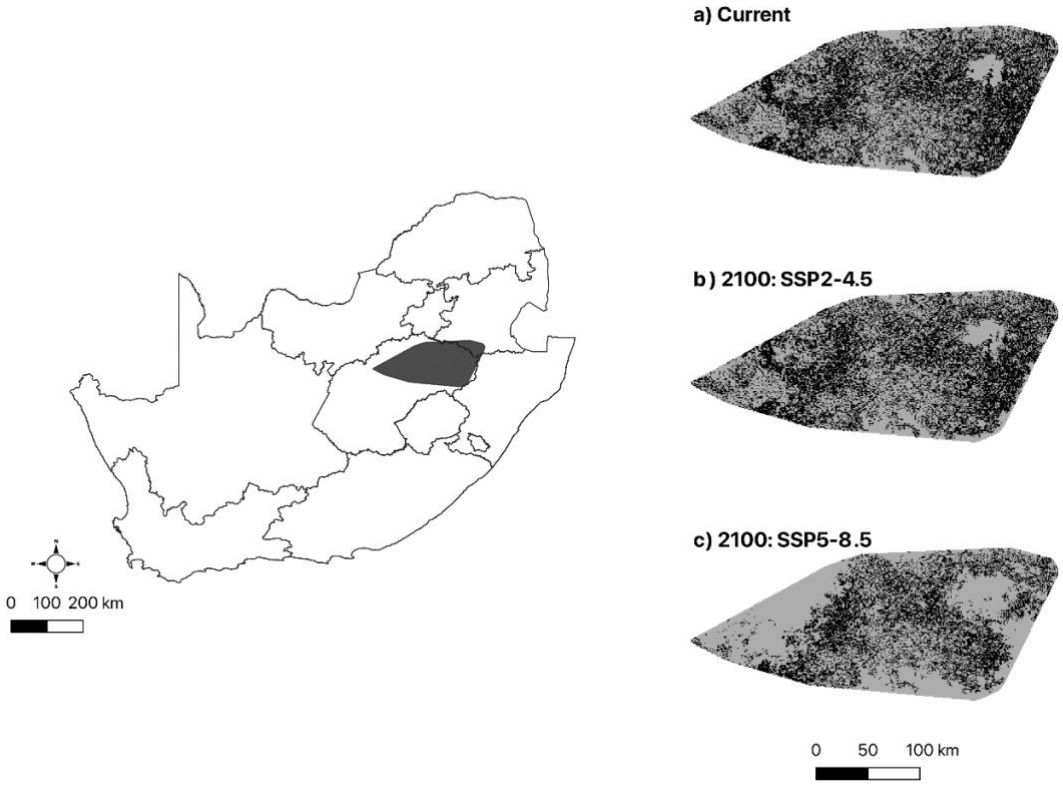


Figure 2.5: Habitat suitability maps showing the predicted distribution of sungazers within their current EOO. Maps shown represent current (a), and future 2100 (moderate case, SSP2-4.5 (b) and worst-case, SSP5-8.5 (c)) predictions. The suitability maps are binary, showing regions which are suitable (black) and unsuitable (grey). SSP = Shared Socioeconomic Pathways.

2.3.3.3. Buffered extent

At the broadscale level, trends in habitat reduction in the buffered extent were similar to the other scale under the SSP245 climatic scenario (Table 2.3). Despite the apparent decreases in those regions, the predicted area of suitable habitat increased by 22% to approximately 30

600 km^2 in the medium-term future (2060) before reducing again in distant futures. By 2100, the area of suitable habitat predicted for sungazers was approximately 28 300 km^2, representing a 13% increase from current predictions (Table 2.3). However, it is important to note that progression through the different futures resulted in a noticeable shift of suitable habitat in a south-west direction, which accounts for the observed increase in suitable habitat in distant futures (Fig. 2.6). Consequently, north-east regions of suitable habitat in current predictions decreased as habitat suitability in south-west regions increased (Fig. 2.6). Under SSP585, reductions in suitable habitat in east, west, south-east and north-east regions were greater than the reductions observed under SSP245 as progression through the different futures occurred (Fig. 2.6). Even though suitable habitat also shifted south-westerly under SSP585, the area of predicted suitable habitat reduced to approximately 20 500 km^2, 18% lower compared to current estimates. Niche overlap was also lower in the buffered extent under both climatic scenarios compared to smaller scales (EOO and interpreted distribution) but reduced through the different futures (Table 2.3). The reduction in niche overlap was also supported by the south-west shift of suitable habitat.

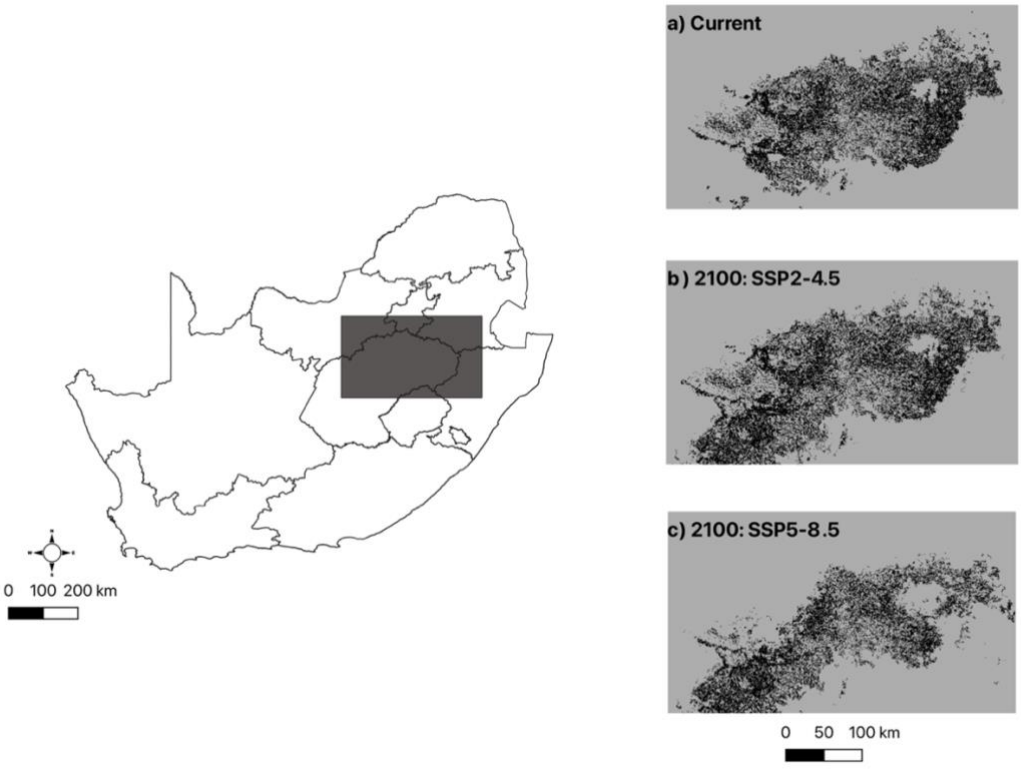


Figure 2.6: Habitat suitability maps showing the predicted distribution of sungazers within the buffered extent of the EOO. Maps shown represent current (a), and future 2100 (moderate case (b) and worst-case (c)) predictions. The suitability maps are binary, showing regions which are suitable (black) and unsuitable (grey). SSP = Shared Socioeconomic Pathways.

Table 2.3: Changes in the predicted suitable habitat of sungazers from current conditions to future climates under different resolutions. Measures for two climate change scenarios (SSP245 and SSP585), at 20-year intervals are shown. Area represents the total area of each resolution. Suitable habitat and proportion suitable depict the area and the proportion (%) of which that area is predicted to be suitable within each resolution. Habitat change (%) shows net gain or loss of habitat. Schoener's D statistic is an estimate of niche overlap between current and future conditions. SSP = Shared Socioeconomic Pathways. EOO = Extent of Occurrence. ID = Interpreted Distribution.

Scenario	Time	Resolution	Area (km²)	Suitable Habitat (km²)	Proportion suitable (%)	Habitat Change (± %)	Schoener's D Statistic
Current	Current	Buffered Extent	142 884	25 028	18	-	-
		EOO	40 573	19 342	48	-	-
		ID	21 985	10 198	46	-	-
SSP245	2040	Buffered Extent	142 884	27 192	19	+9	0,888
		EOO	40 573	19 555	48	+1	0,978
		ID	21 985	10 149	46	0	0,992
	2060	Buffered Extent	142 884	30 612	21	+22	0,799
		EOO	40 573	19 709	49	+2	0,974
		ID	21 985	10 149	46	0	0,991
	2080	Buffered Extent	142 884	26 213	18	+5	0,840
		EOO	40 573	17 755	44	–8	0,915
		ID	21 985	9 594	44	–6	0,940
	2100	Buffered Extent	142 884	28 315	20	+13	0,830
		EOO	40 573	18 608	46	–4	0,955
		ID	21 985	9 910	45	–3	0,970
SSP585	2040	Buffered Extent	142 884	27 225	19	+9	0,893
		EOO	40 573	19 567	48	+1	0,978
		ID	21 985	10 103	46	–1	0,988
	2060	Buffered Extent	142 884	29 865	21	+19	0,826
		EOO	40 573	18 787	46	–3	0,964
		ID	21 985	9 879	45	–3	0,967
	2080	Buffered Extent	142 884	25 656	18	+3	0,817
		EOO	40 573	16 627	41	–14	0,855
		ID	21 985	9 213	42	–10	0,902
	2100	Buffered Extent	142 884	20 499	14	–18	0,631
		EOO	40 573	12 541	31	–35	0,646
		ID	21 985	7 705	35	–24	0,755

2.4. Discussion

I assessed the potential impact of climate change on habitat suitability of *S. giganteus* under two climate change scenarios at 20-year intervals up to 2100. In general, the 'Middle of the Road' (moderate case) scenario did not appear to have a significant impact on habitat suitability for the species, but the 'Taking the Highway' (worst-case) scenario did. The models predicted that by 2100 sungazers could lose a quarter of their suitable habitat within their current interpreted distribution. This prediction only accounts for changing climatic conditions, and not future land use developments, which presumably will have an adverse effect on suitable habitat for the species. At broader scales, models reveal a south-west shift of suitable habitat suggesting that the species could shift their current geographic range in this direction, tracking suitable conditions. However, given their life history and low dispersal ability (Van Wyk, 1992), it is unlikely that climate tracking will be an option. The results of my study support the hypothesis that under worst-case climatic scenarios, the predicted loss of suitable habitat could result in extirpations of many sungazer subpopulations. Although modelling the future distribution of a species may identify potential changes, results must be interpreted with caution. Thus, the combined effect of climate change and land use could be detrimental to the survival of the species, highlighting the need for careful conservation of the species, particularly in central regions of their current distribution.

Sungazers do not appear to be particularly vulnerable under SSP245 (moderate case), but vulnerability increases under the SSP585 (worst-case) scenario. Habitat suitability within the interpreted distribution for sungazers was only marginally affected under the moderate case scenario, with an observable range contraction predicted in the south-east region of their distribution. The same is predicted under the worst-case scenario but not only are contractions amplified in this scenario, but they are also predicted to occur in the western regions of their interpreted distribution. Although the predicted loss of suitable habitat within the interpreted distribution of the species was minimal in medium-term futures, the loss of suitable habitat appears to accelerate in longer term futures with sungazers predicted to lose a quarter of their suitable habitat by 2100, especially if there are limited mitigation measures to reduce the effects of climate change. This suggests that subpopulations of sungazers in the south-eastern and western regions of their distribution may be at risk of becoming locally extinct. It is important to note that these are climate-based predictions and do not account for potential changes in land use such as agricultural activity and mining, both of which are prominent within the species distribution (DEAT, 2005; McIntyre, 2006). Thus, while my

predictions under the moderate case scenario suggest a relatively low impact outcome for sungazers, worse scenarios could be detrimental to the species, especially when coupled with existing anthropogenic pressures that sungazers face (Jacobson, 1989; Mouton, 2014; Parusnath et al., 2017).

Similar patterns of range contraction within the interpreted distribution of sungazers, under both climate change scenarios and time intervals, were observed at broader scales (EOO and buffered extent). However, at these scales further interpretations could be made. For example, despite observable range contractions, habitat suitability increased within medium-term futures, but the loss of suitable habitat was countered by a gain in suitable habitat in the south-west regions, most noticeable within the buffered extent. Although the net amount of suitable habitat was predicted to decrease again in further futures, gains were still prevalent within the south-west regions of the EOO and buffered extent. Such predictions suggest that sungazers could respond to warming climates by expanding their geographic range south-westerly, tracking suitable climates. By comparison, if habitat suitability was only examined within the interpreted distribution of sungazers, evidence for potential climate tracking would not be revealed. Thus, by modelling the distribution of sungazers at a buffered extent, and then overlaying finer extents onto the predictions, not only allows for interpretation at multiple scales, but also demonstrates the importance of selecting an appropriate scale to model the distribution of a species, especially if predictions about a species future distribution are to be made. However, the degree to which scale affects predictions of habitat suitability goes beyond the scope of this study.

This is the first study to model the potential impact that climate change may have on habitat suitability of *S. giganteus*. However, the modelling procedure is complex and multifaceted, and can often lead to uncertainty when interpreting the predictions (Gould et al., 2014; Tang et al., 2018). Thus, species-specific tuning of correlative ENMs is critical (Anderson and Gonzalez Jr., 2011; Kaky et al., 2020). By spatially filtering occurrence records of sungazers (Aiello-Lammens et al., 2015), and incorporating ecologically relevant predictor variables (Anderson and Gonzalez Jr., 2011; Radosavljevic and Anderson, 2014; Guevara et al., 2018), my models had a strong predictive performance. It is also important to note that, although arbitrary, careful selection of the extent in which a species distribution is modelled must be made (Anderson and Raza, 2010). While this study has shown the significance of modelling from a buffered extent (from the EOO) to provide insights into range expansion, choosing an

extent that is too large and includes areas where dispersal may be limited because of geographic barriers or biotic interactions that may result in reduced performance of correlative ENMs (Anderson and Raza, 2010). Given the good performance of the models in this study, the buffered extent used appeared to be reasonable, and provided valuable insights into how sungazers could respond to climate change. Overlaying natural grassland onto the predictions also provided important information regarding areas that are suitable for sungazers, which will be important in future conservation planning.

When assessing a species vulnerability to climate change, the use of hybrid-ENMs (correlative and mechanistic models, e.g., Meineri et al., 2015; Gamliel et al., 2020; Mi et al., 2022), can provide a more informative assessment of a species vulnerability to climate change. However, as in this study and many others (e.g., Houniet et al., 2009; Guo et al., 2021; Petford and Alexander, 2021), a lack of behavioural and physiological data of a species may limit the use of hybrid-ENMs. Nevertheless, even though correlative models may not be definitive, when fine-tuned, they do provide an indication of what the future distribution of a species could be under climate change, and may enhance conservation efforts (Raxworthy et al., 2003; Guisan and Thuiller, 2005; Petford and Alexander, 2021).

Despite the use of a correlative model in this study, by examining known life history traits of sungazers, inferences about their ability to respond to climate change can still be made. Sungazers are habitat specialists that display high burrow fidelity, rarely stray far from their home burrows (Van Wyk, 1992; Stanton-Jones, 2018), and individuals have been found occupying the same burrow at least 16 years (see chapter 3). This philopatric nature suggests that the species has low vagility and because of this, may not be able to track suitable conditions. In addition, because a significant portion of sungazer habitat has been fragmented due to habitat transformation through anthropogenic activity (Branch, 1988, Parusnath et al., 2017), dispersal capacity may further be reduced (Saunders et al., 1991; Honnay et al., 2002; Opdam and Wascher, 2004, Robillard et al., 2015). Even if the effects of anthropogenic habitat transformation are ignored, geographic barriers such as wetlands, dams, rivers, and mountain ranges may also prevent dispersal into suitable areas (Parusnath et al., 2017). Therefore, it is unlikely that sungazers will be able respond to climate change by shifting their geographic range.

Species living in fragmented habitats are more vulnerable to the effects of climate change than those that are not (Travis, 2003). Dispersal limitations because of fragmented habitats not only affects the ability of a species to track suitable conditions, but the associated reduction of gene flow among populations, and a loss of genetic diversity within populations (Frankham, 2006; Parusnath, 2020), may compromise a species ability to evolve adaptations in response to climate change. In addition, evolving adaptations would require a long time. Since sungazers are long-lived, have low fecundity, long generation lengths, and limited dispersal capacity (Van Wyk, 1992), keeping pace with rapid climate change through genetic adaptation appears unlikely (Dunham an Overall, 1994; Sinervo et al., 2010), especially considering that the effects of historical habitat fragmentation have not yet manifested in the genetics of sungazers (Parusnath, 2020). Given that reduced genetic diversity in sungazers, as a result of habitat fragmentation, may only be observed within the next ~120 years (Parusnath, 2020), it seems unlikely that they will evolve adaptations in response to changing climates within the next century.

Range contractions and distribution shifts are common predicted responses to climate change among reptiles (e.g., Araújo et al., 2006; Houniet et al., 2009; Moreno-Rueda et al., 2012; Petford and Alexander, 2021). However, as with the predictions of this study, the ability to track suitable climates may be compromised in habitat specialists. In such cases, behavioural plasticity may be an appropriate response to shifting climate. Sungazers are efficient thermoregulators and can achieve target body temperature over a wide range of environmental conditions through simple behavioural adjustments (Stanton-Jones et al., 2018). This suggests that behavioural plasticity may assist the species in coping with changing climates. However, changes in behaviour and activity patterns to compensate for a warmer environment may have eco-physiological implications (Sinervo et al., 2010): (i) reduced activity outside of burrows may restrict foraging time, (ii) prey abundance may be limited during foraging periods, (iii) growth rates may be reduced, and (iv) aspects of reproduction such as mate acquisition and embryonic development could be compromised. However, more studies relating sungazer behaviour to warming temperatures is required to enhance current predictions of their vulnerability to climate change.

The predicted range contractions under both climate change scenarios, and the unlikelihood that sungazers will track suitable conditions, suggests that conservation management for the species is critical. Although the current suitable habitat for sungazers remains severely

fragmented, Parusnath et al. (2017) reported a significant reduction in the rate of transformation of natural grassland within the current distribution of sungazers. However, there are still some important considerations: (i) there is much uncertainty as to how landowners will modify agricultural practices under changing climates, and (ii) sungazer distribution falls within parts of South Africa where rates of incoming solar radiation are relatively high (Fluri, 2009; Singh, 2016), and could support developments of solar power plants. While renewable energy resources are important to mitigate the effects of climate change, their implementation may fragment suitable habitat for sungazers even further. Thus, careful selection of areas to develop renewable energy systems is required to mitigate any associated threats to remaining sungazer subpopulations.

The Endangered Wildlife Trust (EWT) have begun conservation efforts through their 'Sungazer Custodianship Programme' whereby landowners sign a 5-year renewable agreement to protect the habitat on their properties where sungazers occur (Gibbons, 2022). It is, however, important to note that this programme may only offer short-term protection for the species. Because of this, EWT are also working to establish protected areas within sungazer distribution through biodiversity stewardship programmes (Gibbons, 2022). The predictions in my study suggest that stewardship programmes should be concentrated within the central and southern parts of sungazer distribution – areas predicted to remain stable under climate change. Although the eastern and western regions of sungazer distribution may become unsuitable in the future, I recommend that monitoring programmes of existing sungazer subpopulations within those regions are implemented to ensure early detection of changes in population dynamics, such that swift conservation action can be taken (Parusnath et al., 2017).

This study has provided the first indication as to how sungazers could respond to of climate change. Although there is much uncertainty associated with modelling the future distribution of a species, examining the life history traits can enhance interpretations of the models. Despite the prediction that sungazer distribution may shift in the future, the species life history traits, and low dispersal capacity suggests that climate tracking may not be possible. When the detrimental effects of habitat fragmentation are considered, sungazers may be more vulnerable to effects of changing climates than what the models predict. Nevertheless, the modelling techniques in this study have provided sufficient evidence to inform conservation planning.

2.5. References

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CHAPTER 3

Habitat transformation correlates with the decline of sungazer (*Smaug giganteus*) subpopulations

ABSTRACT

A major threat to the survival of many reptile species is the consequence of rapid growth of the human population. The acceleration of associated anthropogenic activities causes fragmented and transformed habitats, placing the persistence of biodiversity in transformed areas at risk. The sungazer (*Smaug giganteus*) is a threatened (Vulnerable) grassland specialist lizard species. Its geographic distribution is significantly impacted by agriculture and mining activities, resulting in major threats to the species. I assessed sungazer population demographics and dynamics at four sites, each with different habitat conditions by resurveying sungazer subpopulations first surveyed in 2004, 16 years later, in 2020. Individuals were marked with Passive Integrated Transponders. Abundance declined by more than 50% at two sites associated with mines and an overgrazed site over the 16-year period, and the proportion of recaptures were also the lowest in these sites (< 15%). Most recaptured lizards were not found in their original burrows, and most lizards in transformed habitats were found more than 100 m away from their original burrows. My results highlight the potentially detrimental effects of habitat transformation on sungazer demographics that have not previously been demonstrated. Previous assessments focused on local extinction of aggregations but not declines in abundance in aggregations that had not yet gone extinct. My results suggest that the species may be more susceptible to habitat transformation than previously estimated. I recommend careful, continuous monitoring of sungazer subpopulations at fine spatial resolutions such that swift conservation action can be taken.

Keywords: cordylid, habitat transformation, grassland, population demographics, population dynamics, *Smaug giganteus*

3.1. Introduction

Although reptiles comprise a significant portion of the world's biodiversity, studies on their extinction risk lag behind those on birds and mammals (e.g., Kerr and Currie, 1995; Loehle and Eschenbach, 2012; Geyle et al., 2018). This has resulted in reptiles being neglected in conservation programs (Böhm et al., 2016; Tolley et al., 2016). However, studies identifying the global population decline of reptiles have gained momentum over the last two and half decades (Gibbons et al., 2000; Böhm et al., 2013; Böhm et al., 2016; Tingley et al., 2016; Cox et al., 2022). Of the 87% of reptile species that have been assessed, 21% are classified as threatened and nearly 20% are data deficient (Cox et al., 2022). While reptiles remain underrepresented, there is sufficient evidence to suggest that the group is gaining a higher profile in conservation.

Natural fluctuations in herpetofauna populations are common (Pechmann et al., 1991; Blaustein et al., 1994), but unnatural declines are cause for conservation concern. Distinguishing between natural and unnatural declines requires long-term population and macroecological studies (Pechmann et al., 1991; Blaustein et al., 1994). The need for land increases as human population expands, resulting in increased associated anthropogenic activities (Hooke et al., 2013). Unfortunately, this can be detrimental to many reptile species (Anderson and Marcus, 1992). Anthropogenic threats such as habitat degradation, increased agricultural activities, the introduction of invasive species, poaching for the pet and muthi trade, pollution, and climate change are amongst the primary drivers of population decline in reptiles (Gibbons et al., 2000; Böhm et al., 2013; Tolley et al., 2016). However, transformation of land resulting from increased agricultural activities is one of the largest contributors that threaten African reptiles (Tolley et al., 2016).

Although one-fifth of all reptile species are at risk of extinction, the levels of threat vary across geographic regions and taxonomic groups (Böhm et al., 2013; Böhm et al., 2016; Cox et al., 2022). For example, a fifth of European reptiles are at risk (Cox and Temple, 2009), but only 5.4% of southern African reptiles are at risk (Tolley et al., 2019). Taxonomically, chelonians appear to be at greater extinction risk while the risk is lowest in snakes (Böhm et al., 2013). While assessor bias may be linked to variation in measures of extinction risk (Hayward et al., 2015; Vignoli et al., 2016), the variation may also depend on the biological traits that species exhibit and environmental factors (e.g., increased annual temperature and precipitation) to which species are exposed. Species with large body sizes, specialized

habitats and restricted ranges tend to be at a greater risk of extinction (Tingley et al., 2013). Foraging mode is another factor that influences susceptibility to extinction with ambush foragers having an increased risk of extinction (Reed and Shine, 2002). Furthermore, it is likely that the combined effects of some of the abovementioned threats further exacerbate the risk of extinction for most threatened species. This is particularly true for many squamates living in geographically restricted habitats that are easily accessible to humans (Böhm et al., 2016).

Sungazers (*Smaug giganteus*) are large-bodied, heavily armoured diurnal cordylid lizards with specific habitat requirements. The species is threatened (Vulnerable; IUCN, 2022) and is endemic to the Highveld grasslands of South Africa, occurring in northern regions of the Free State, and southernmost parts of the Mpumalanga provinces (De Waal, 1978; Jacobson, 1989). Sungazers occur in well-defined aggregations (often referred to as colonies; see Jacobson, 1989) in the landscape, and distances between aggregations can be relatively great (Stolz and Blom, 1981, Jacobson, 1989, Van Wyk, 1992, Parusnath, 2014). Individuals appear to be highly philopatric (Van Wyk, 1992; Stanton-Jones, 2018), at least in the short-term. I defined a subpopulation of sungazers as all individuals occurring within an aggregation. Because sungazers occur only within the agriculturally dominated regions of the country (DEAT, 2005), the species is greatly exposed to the detrimental impacts of habitat transformation and population fragmentation (Jacobson, 1989; Mouton, 2014). Since sungazers have never been recorded recolonizing any form of rehabilitated or fallowed land, habitat loss may be irreversible (Van Wyk, 1992, Parusnath, 2014). More than one-third of sungazer subpopulations have already been driven to extinction over the last four decades (Parusnath et al., 2017), with the decline being attributed to an increase in commercial agricultural development, and the illicit pet and muthi trade. Although Parusnath et al. (2017) assessed declines in the number of aggregations (i.e., the percentage of aggregations that have gone extinct), it is likely that the impact of habitat degradation (i.e., abundance within subpopulations) has also caused declines within subpopulations. Thus, Parusnath et al.'s (2017) estimate of decline may underestimate the actual rate.

Unlike other members of the Cordylidae family, sungazers live in self-constructed burrows in *Themeda trianda* grassland (Bates et al., 2014; Parusnath, 2014). They are strict ambush foragers, rarely moving more than 2 m from burrow entrances (Van Wyk, 1992; Ruddock, 2000; Stanton-Jones, 2018). Unfortunately, this sedentary lifestyle, large body size, k-

selected life history, habitat specialization, and the relatively small geographic range increases the species vulnerability to anthropogenic threats such as habitat transformation and poaching (Tingley et al., 2013; Böhm et al., 2016; Parusnath et al., 2017, IUCN, 2022).

I resurveyed four sungazer subpopulations that were initially surveyed in 2004. I assessed how sungazer population demographics and dynamics have changed over the 16-year period between surveys, and assessed the impact of habitat transformation on subpopulation size by comparing abundance from 2004 and 2020. Assessments were limited to aggregations for which I had historical measures (see McIntyre, 2006). Two of the sites were located near to mine tailing dumps, a third in overgrazed rangeland, and a fourth in undisturbed rangeland. I acknowledge the relatively low statistical power of this analysis as a result of the limited number of subpopulations that were available for assessment. Nevertheless, my assessment provides unique insights into how the sungazer population has changed over a 16-year period, and how habitat conditions appear to have influenced those changes. Given the vulnerability of the species to anthropogenic activity, I tested the hypothesis that the mine sites would show the greatest declines in sungazer abundance. Since anecdotal evidence suggests that *S. giganteus* usually occurs within patches of short *T. trianda* grassland (Parusnath *et al.*, 2017), I also predicted that the subpopulation on the overgrazed rangeland would be most stable.

3.2. Methods

3.2.1. Study site

I resurveyed the four study sites within the Free State Province of South Africa, which were originally surveyed in an assessment of heavy metal contamination in *S. giganteus* due to the presence of mine tailings (McIntyre, 2006), to measure changes in abundance between these time periods. Two sites, Mine 1 and Mine 2 were situated near the town of Welkom, while the Overgrazed Rangeland site was situated between the towns of Kroonstad and Welkom. The most natural site, Undisturbed Rangeland, was located near the town of Lindley (exact localities are not provided due to the threatened status of the species on recommendation of the South African National Biodiversity Institute [SANBI], 2022). All sungazers were marked with Passive Integrated Transponders (PITs) during the original 2006 survey, and previously unmarked individuals were similarly marked in the recent survey.

The four study sites each had different characteristics which allowed for assessment of the impact of different habitat conditions on *S. giganteus* abundance. A natural saltpan existed at

the Mine 1 site. The pan and the surrounding soils had been subjected to the licensed discharge and evaporation of gold mine water for several decades (Weiersbye et al., 2003; McIntyre, 2006). Consequently, Mine 1 (area: 2.02 km^2) was contaminated, and observations reported by McIntyre (2006) suggested that a reduction in the abundance of *S. giganteus* had already occurred at this site. The Mine 2 site (area: 0.16 km^2) contained only a small number of individuals and was located adjacent to slimes dams and was thus impacted by acid mine drainage (McIntyre, 2006). However, inorganic contaminants in water, soils, sediments and vegetation were at lower concentrations at Mine 2 than Mine 1 (McIntyre, 2006). By contrast, the Overgrazed Rangeland (area: 1.51 km^2) and Undisturbed Rangeland (area: 0.15 km^2) sites were relatively free from mine contaminants (McIntyre, 2006). The Overgrazed Rangeland site, which was located on a game farm, was severely overgrazed due to the high abundance of grazers but had recently partially recovered. The Undisturbed Rangeland site remained free from grazers over the survey period.

3.2.2. Experimental design and protocol

3.2.2.1. Sungazer sampling

The first survey was conducted during February, September and October 2004 (McIntyre, 2006). I conducted the second survey between November 2016 and March 2020 in which I located marked burrows from the first survey with the purpose of quantifying the number of marked lizards that remained within each study site. Following methods used by Parusnath et al. (2017), I carefully resurveyed each site to ensure that I detected all sungazer burrows. Briefly, I walked line transects 5 m apart to cover the entire site and located sungazers by the presence of their burrows. Burrows were confirmed occupied if there was evidence of activity; for example, tail/claw markings, presence of scales, burrow entrances clean from debris, or in uncertain cases I inserted a borescope camera (Bosch GIC 120 C) into burrows to confirm the presence of lizards.

I deployed traps at all occupied burrows and monitored them every 10 minutes to minimize any stress on captured lizards. Traps consisted of an iron nail fixed to the roof of burrow entrances and two string nooses fitted in parallel at the entrances. All captured lizards were scanned for PITs using the EasyTracer FDX/HDX Reader, and individuals not already marked with PITs were marked with a subcutaneous injection of a PIT into the postero-fermoral region of the hind legs using the same methods described in McIntyre (2006) and Stanton-Jones (2018). Prior to PIT insertion, the injection site was cleaned using F10

disinfectant spray. Following the injection of a PIT, the open wound was cleaned using F10 disinfectant topical cream. I also recorded morphometric measures, sex, age (juvenile/adult), GPS coordinates and PIT IDs of captured adult lizards. Since morphological sexual dimorphism exists in adult sungazers (Van Wyk, 1992), sex could easily be identified by the presence of generation glands on the ventral surfaces of adult male limbs. However, I could not identify the sex of juvenile sungazers using field techniques (Van Wyk, 1992). To avoid any potential injury, juvenile sungazers with a body mass less than 100 g and a snout-vent length smaller than 125 mm were not marked with PITs but morphometric measures were still recorded. All individuals were released into their home burrows after processing.

3.2.3. Statistical analyses

Statistical analyses were conducted using *R* 4.1.1 (R Core Team, 2021).

3.2.3.1. Recapture analysis

During surveys, the number of recaptured lizards at each study site was recorded. Lizards that were not found during the second survey were assumed to no longer occur at the site. The proportion of recaptures from the overall original sample was compared using a proportion z-test. I also compared recapture rates in relation to the number recorded in the first survey for each site, and between sex using Pearson's Chi-square tests.

A Pearson's Chi-square test was conducted to compare the proportion of each sungazer subpopulation that had moved from their original home burrows to the proportion of those that were found in their original burrows between the different study sites. Thus, I compared the differences between the number of recaptured lizards that had moved to those that were recorded in the same burrow in the two surveys. I did the same for comparison between sex. The GPS coordinates of sungazers captured in the original survey and recaptures were plotted on Google Earth (Version 7.3.4.8248), and distances between the GPS coordinates in the original captures and the GPS coordinates of our recaptures were measured using the ruler function**.** Lizards that had not moved from their original burrows were assigned a distance of 0 m for distance moved. Because the distance data did not meet the assumptions of normality ($P < 0.05$), I log-transformed the measures. A two-factor analysis of variance (2-way ANOVA) was then performed to compare distances that sungazers moved, with study site

and sex as factors for comparison. I excluded Mine 2 from these analyses as only a single lizard was recaptured which did not permit the calculation of variance.

3.2.3.2. Population analysis

I estimated the percentage change of sungazer numbers at each study site, and calculated the loss or gain of individuals within each site between the two surveys using the difference in the number of sungazers originally captured and those captured in the second survey. For these measures, juvenile lizards, and lizards that were not captured but burrows were confirmed occupied, were included. I then calculated the proportional difference between surveys of the abundance of adult male and female sungazers at each study site, and used a generalized linear model (GLM) with a quasibinomial distribution to test for differences between sex, and between study sites. Because juvenile lizards were not recorded in the first survey, and there is a small chance that lizards may have been missed during the survey, I treated the first survey as a minimum number of sungazers present within the study site. Thus, the potential decline of sungazers was considered to be a conservative estimate, while any potential increases were considered to be maximum increases. To test for deviation from the expected 1:1 (Male : Female) sex ratio, two-tailed binomial tests were performed on current sex ratios within the different sites. Since juvenile sungazers were often too small for sex to be identified, they were excluded from comparative sex analyses.

3.3. Results

The abundance of sungazers recorded across all sites reduced from a minimum of 198 to 107 individuals (89 captured adults, six uncaptured adults, and 12 juveniles) between surveys. The majority of these (n = 84) were new/unmarked individuals. Details of numbers at each site are provided in Table 3.2.

3.3.1. Recaptures

Twenty-three of the sungazers (Mine 1: n = 7, Mine 2: n = 1, Overgrazed Rangeland: n = 6, Undisturbed Rangeland: n = 9) marked in the first survey were recaptured. Relative numbers of recaptures differed between study sites (X^2 = 10.37, df = 3, $p < 0.05$), but not between sexes (X^2 = 2.71, df = 3, p = 0.44). In general, the proportion of recaptures between surveys was low and less than a third of the lizards recorded in the first survey were recorded in the second for each site (Table 3.1). The greatest proportion of sungazers were recaptured at the Undisturbed Rangeland (28%) compared to the other sites where the proportion of recaptures

was less than 15% (Table 3.1). Even though Mine 2 had the second highest proportion of recaptures at 14%, it is worth noting that only a single lizard (male) was recaptured from the site's first survey, which was already a small subpopulation at this time (n = 7). Both Mine 1 and the Overgrazed Rangeland had the lowest proportion of recaptures (8%; Table 3.1).

Of the 23 sungazers recaptured, 18 were not recaptured in their original burrows. The relative number of lizards that moved to different burrows did not differ significantly between sites (X^2 = 3.78, df = 3, p = 0.29), nor between sex (X^2 = 2.62, df = 3, p = 0.45). However, at Mine 1, the lowest proportion of sungazers moved (57%), while at Mine 2 and Overgrazed Rangeland, all recaptured lizards had moved from the burrows in which they were originally captured. Undisturbed Rangeland had the largest sample of recaptures (n = 9), and 78% of these recaptures were not caught in the burrows from where they were initially found (Table 3.1).

Although not significantly different ($F_{(2,16)}$ = 1.25, p = 0.31), the recaptured lizards at Mine 1 moved, on average, the furthest distances from their original burrows ($\bar{x}$ ± SD = 195.4 ± 309.1 m), followed by the lizards at the Overgrazed Rangeland ($\bar{x}$ ± SD = 111.6 ± 131.5 m) and Undisturbed Rangeland ($\bar{x}$ ± SD = 23.8 ± 25.9 m). There was no significant difference in the distances moved between sexes ($F_{(2,16)}$ = 0.08, p = 0.78), nor in the interaction of site and sex ($F_{(2,16)}$ = 0.88, p = 0.43). However, on average and compared to males, there was a trend for female sungazers having moved further distances from their original burrows at all sites except for at Undisturbed Rangeland (Table 3.1).

Table 3.1. A comparative summary showing the total number of sungazers recorded by McIntyre (2006) and those recaptured during this survey from each study site. The proportion of sungazers that were recaptured are shown, along with the proportion of recaptured sungazers that moved and the average distances (± SD) that they moved.

Site	Sex	Recorded (n)	Recaptures (n)	Recaptures (%)	Moved (%)	Distance moved ($\bar{x}$ ± SD m)
Mine 1		**86**	**7**	**8**	**57**	**195.4 ± 309.1**
	Male	25	2	8	50	5.1[1]
	Female	61	5	8	60	271.5 ± 343.4
Mine 2		**7**	**1**	**14**	**100**	**21.2[1]**
	Male	4	1	25	100	21.2[1]
	Female	3	0	0	0	-
Overgrazed		**73**	**6**	**8**	**100**	**111.6 ± 131.5**
	Male	31	2	6	100	95.7[1]
	Female	42	4	10	100	119.5 ± 161.9
Undisturbed		**32**	**9**	**28**	**78**	**23.8 ± 25.9**
	Male	14	5	36	80	31.2 ± 30.9
	Female	18	4	22	75	14.6 ± 17.8
Total:		**198**	**23**	**12**	**78**	**126.3 ± 206.6**
	Male	74	10	14	80	47.4 ± 48.8
	Female	124	13	10	77	189.4 ± 262.3

[1]*Standard deviation measures not reported due to low sample size.*

3.3.2. Population change

Overall, the relative sizes of the surveyed sungazer subpopulations were smaller in the second survey compared to those in the first survey, with study site having a significant effect (X^2 = 10.78, df = 3, $p < 0.05$; Fig. 3.1; Table 3.2). Sungazer numbers at Mine 1, Mine 2, and Overgrazed Rangeland experienced a minimum decline of more than 50% between surveys (Table 3.2). By contrast, Undisturbed Rangeland was the only site in which sungazers increased (3%) in number between surveys (Table 3.2). However, given that juvenile sungazers were not recorded in the first survey, the marginal increase in the number of sungazers at this site was considered to be a maximum increase.

When comparing sex ratios between the two surveys, the numbers of female sungazers appeared to have reduced more than males, although this trend was not significant (X^2 = 1.91, df = 1, p = 0.17; Fig. 3.1; Table 3.2). Proportionally, Mine 1 and Mine 2 showed the greatest loss of female sungazers (74% and 100%, respectively), while the Undisturbed Rangeland showed the lowest loss (17%; Fig. 3.1; Table 3.2). There was a trend for more male sungazers being lost at the Overgrazed Rangeland than females, but the number of male sungazers at the Undisturbed Rangeland remained unchanged (Fig. 3.1.; Table 3.2). All sites had sex ratios that did not deviate significantly from the expected 1:1 sex ratio (Table 3.2). However, at the Overgrazed Rangeland site sungazers had a sex ratio skewed in favour of females, although the deviation was not significant (p = 0.14). At Mine 2, only male individuals were recorded within the small subpopulation of sungazers (Table 3.2).

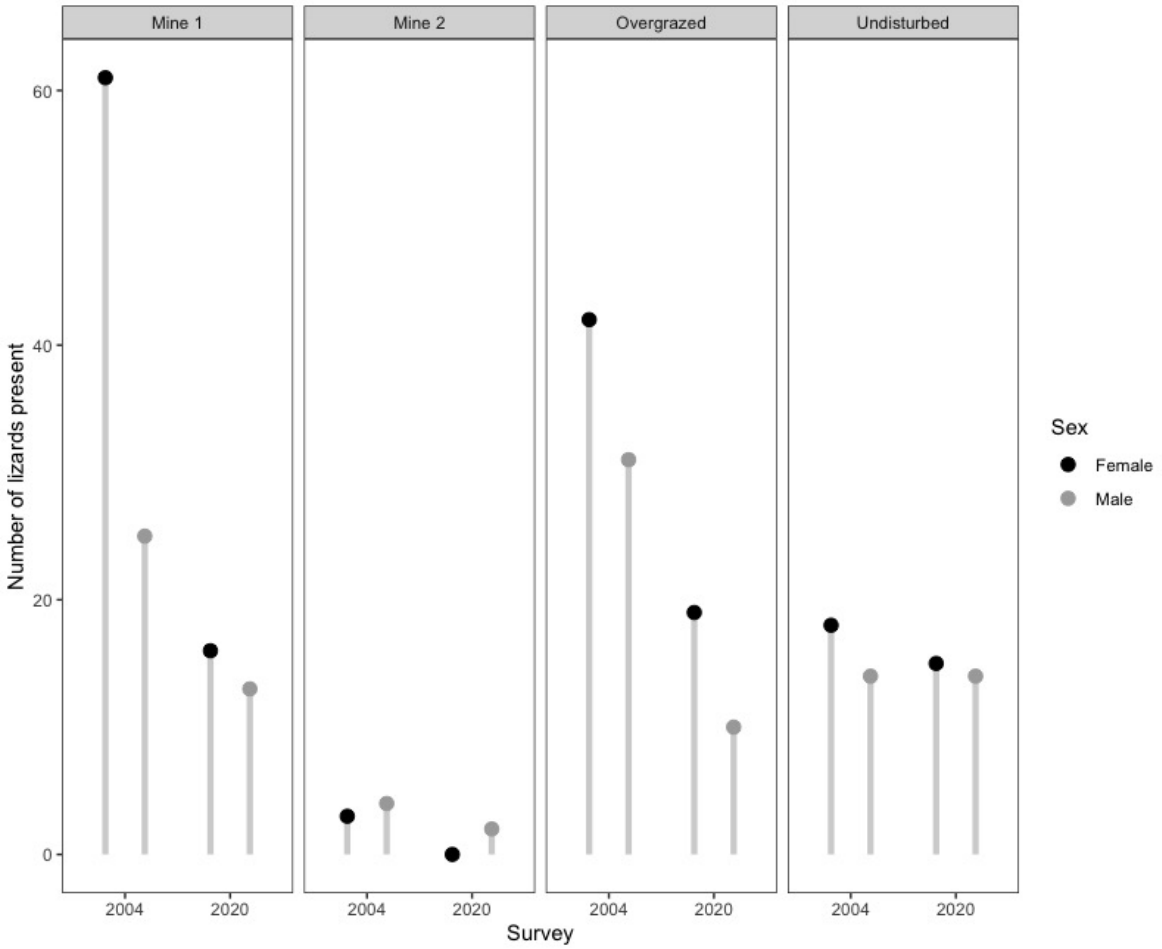


Figure 3.1. The abundance of adult sungazers (male and female) that were present within each study site during the first (2004) and second survey (2020).

Table 3.2. A summary of sungazer subpopulation demographics at each study site. Total counts include juvenile sungazers, and those that were not captured but burrows were confirmed active. Abundance change (–: decrease; +: increase) in the subpopulation of sungazers (overall and sex) at each site is shown. Current sex ratios (M:F) with statistical significance from binomial tests are also included.

Site	Sex	First Survey (n)	Second Survey (n)	Percentage change (%)	Current sex ratio (M:F)	P-value
Mine 1		**86**	**39**	**–55**		
	Male	25	13	–48	**1:1.2**	**0.71**
	Female	61	16	–74		
Mine 2		**7**	**3**	**–57**		
	Male	4	2	–50	**1:0**	*
	Female	3	0	–100		
Overgrazed		**73**	**32**	**–56**		
	Male	31	10	–68	**1:1.9**	**0.14**
	Female	42	19	–55		
Undisturbed		**32**	**33**	**+3**		
	Male	14	14	0	**1:1.1**	**1.00**
	Female	18	15	–17		
Total:		**198**	**107**	**–46**		
	Male	74	39	–47	**1:1.3**	**0.29**
	Female	124	50	–60		

**Binomial test was not run for the sex ratio at Mine 2.*

3.4. Discussion

I assessed demographic changes between two surveys (2004 and 2020) of four *S. giganteus* subpopulations, each under different habitat conditions. In general, recapture rates for the period were lowest in transformed habitats, and the overall size of the sungazer subpopulations in these habitats decreased most dramatically over the survey period. Abundance in the habitat that was most natural and not disturbed may have increased marginally over the period. Despite the trend of more female sungazers being lost from subpopulations associated with mine contaminated sites than males, the apparent reduction did not result in a male-biased sex ratio. Even though most recaptured lizards were found in burrows more than 100 m from where they were originally caught, there appears to be no significant link between habitat conditions and burrow fidelity and behaviour. The results of this study support the hypothesis that at a single subpopulation level, populations of *S. giganteus* appear to have declined due to habitat deterioration. Thus, studies such as Parusnath et al. (2017) which estimated the proportion of subpopulations which had become locally extinct probably underestimate the actual decline in the total population number of *S. giganteus*.

Recapture rates of *S. giganteus* individuals between the first and second survey were relatively low suggesting significant population turnover over the 16-year period. However, given that I did record several recaptures over this timeframe, it confirms that sungazers are long lived. Given the 16-year period between surveys, and by assuming that my recaptures were of individuals originally marked at early maturity (~5 years), my data indicate a longevity of more than 21 years for sungazers living in the wild. Recapture rates also appear to be associated with habitat condition, with the lowest proportion of recaptures being recorded in mine contaminated and overgrazed habitats. Low recapture rates in these habitats suggest that life expectancy of sungazers living there may be reduced. However, since the exact age of when the sungazers were first captured and marked is unknown, this trend should be considered highly suggestive but speculative. Even though the highest proportion of recaptures were recorded in natural, undisturbed conditions, recaptures made up a relatively low proportion of captures, suggesting that the large time gap between the first and second survey at this site may have had an impact. Nevertheless, because the proportion of recaptures within the disturbed habitats were at least half of those under natural conditions, it is possible that the quality of habitat was more influential than the time gap between surveys.

The comparison between the overall size of the current population and the initial population when individual sites are considered provides evidence that at least some subpopulations of *S. giganteus* are declining at a local scale. Given the history of the effects of mining on the environment (Allan, 1995; Rybicka, 1996; Agboola et al., 2020; Worlanyo and Jiangfeng, 2021), and on sungazers (McIntyre and Whiting, 2012), the significant decline in abundance at mine contaminated habitats was expected. However, since anecdotal evidence suggests that sungazers are more commonly found in short grass patches (see Chapter 4), the decline within the overgrazed habitat was unexpected. This suggests that although the habitats have been transformed differently, the impact on subpopulations can be similar. At the Undisturbed Rangeland site, where habitat conditions were considered most stable and natural, I observed a similar abundance of sungazers between the two surveys. Thus, my findings provide evidence for the detrimental impact that transformed habitats can have on populations of philopatric reptiles such as sungazers.

Although not statistically significant, the overall net loss of female sungazers appeared to be greater than the loss of males across the different habitat conditions. The greatest reduction of female sungazers was observed at mine contaminated sites suggesting that females may be more vulnerable to the effects of habitat transformation and fragmentation caused by mine contaminants than males. In overgrazed habitats, however, the impact appears to be similar across sex but a larger sample of lizards in these habitats is needed to confirm this finding. Even though the reduction of female sungazers was seemingly greater than males at most sites, sex ratios were largely unaffected. Instead, the loss of female sungazers at Mine 1 resulted in a sex ratio closer to the expected 1:1 sex ratio than was reported in the first survey (McIntyre, 2006). While the current sex ratio at Mine 1 is not yet concerning, the reduction of females at the site is. Although the causal link of the decline needs to be identified, I suspect that if the female numbers at this site were to continue a downward trajectory, the survival of that subpopulation will become compromised. This prediction is supported by the current subpopulation at Mine 2. Since no female sungazers were found at Mine 2, reproduction at this site is uncertain as only two males and an uncaptured individual were found. Thus, the data from this site suggests that this subpopulation is likely to soon become locally extinct.

The majority of recaptured sungazers at all four sites were not found in burrows from where they were originally captured. This suggests that burrow fidelity and behaviour may not necessarily be influenced by the condition of the habitat. It is possible that sungazer burrows

have a limited lifespan; when they collapse, sungazers may be forced to seek alternative sites in which to construct new burrows. Nevertheless, the relatively low burrow fidelity that I observed was unexpected as sungazers have typically been viewed as sedentary ambush foragers with generally high burrow fidelity (Van Wyk, 1992; Ruddock, 2000; Stanton-Jones, 2018). However, since burrow fidelity has never been assessed over a decades-long temporal scale, it is possible that this finding is the norm over long time spans. Even though sungazer displacement in transformed habitats was, on average, more than 100 m, variation among subpopulations was high. It is also worth noting that female sungazers appeared to moved further distances compared to males in transformed habitats, particularly those subjected to mine contamination. Although the trend was not statistically significant, such behaviour could be linked to aspects of reproductive biology (Sasaki et al., 2015). Despite the trends seen in my data, the effects of habitat transformation on sungazer behaviour remains unclear.

This is the first study to provide insights into the effects that habitat transformation and fragmentation has on sungazer abundance at fine spatial resolutions. However, a lack of annual surveys between 2004 and 2020 results in some limitations. Specifically, the annual population turnover rate cannot be estimated with accuracy and was therefore excluded from analysis in this study. In addition, regular surveys throughout the 16-year period would have allowed for an assessment of the rate at which sungazer subpopulations are declining and how habitat conditions are affecting that rate. Nevertheless, these surveys provide the most complete dataset of marked sungazers and their burrows at specific sites, but it is advised that future assessments are done carefully as the condition of the veld may affect the detectability of burrows. However, the method that I used, and was described by Parusnath et al. (2017), is likely to detect all sungazer burrows. My study only made use of four available study sites which does result in low statistical power, and I therefore caution against overinterpretation of the reported trends. Despite some limitations, and the low sample of sungazer subpopulations, my study provided the first assessment of sungazer demographics over a decades-long temporal scale, and has highlighted the need for continuous monitoring of sungazer subpopulations. This study has also revealed the potentially detrimental effects that habitat transformation and fragmentation can have on sungazer abundance.

Low recapture rates and a decline in sungazer numbers provides further evidence that habitat specialists are particularly vulnerable to the effects of habitat fragmentation as reported by Andrén et al. (1997), Henle et al. (2004), Keinath et al. (2017), and Walkup et al. (2017).

Low recapture rates in fragmented habitats have been reported in *Sceloporus arenicolus* (Dunes sagebrush lizard) and *Holbrookia maculata* (Lesser earless lizard), with *S. arenicolus* also being a threatened habitat specialist (Walkup et al., 2017). Generalist species, however, appear to be less impacted by habitat fragmentation as even in highly fragmented habitats, recapture rates are high and population demographics remain relatively stable, presumably because of their life histories (Fitzgerald et al., 1999; Walkup et al., 2017). Although it may be argued that the low recapture rates of sungazers in this study could be explained by individuals simply dispersing to more suitable habitats, the discreet aggregation of burrows, their life history (Van Wyk, 1992), the generally high burrow fidelity of the species (Stanton-Jones, 2018) and the finding that many individuals were still found in the same habitat after more than one and a half decades suggests potentially severe effects of habitat fragmentation on *S. giganteus* subpopulations over this period. Thus, it is evident that sungazers face an increased risk of extinction in fragmented habitats. This prediction is also supported by Henle et al. (2004) who suggests that habitat specialists, and species with generally low dispersal ability living in fragmented habitats are more at risk of extinction than generalist species.

Stanton-Jones (2018) reported that male sungazers moved greater distances compared to females, which contradicts the findings of this study, particularly at mine contaminated sites. While differences in my findings may potentially be driven by habitat conditions, with a sample size of only four study sites, statistical power is relatively low, and realistically my findings in low quality habitats may instead be more closely related to aspects of reproduction. Comparatively, however, habitat conditions at the Undisturbed Rangeland were more similar to those in Stanton-Jones (2018), and the movement patterns of sungazers at this site were also similar, even though burrow fidelity was lower. Given the short distances travelled by the lizards at the undisturbed site, it is possible that the individuals did not permanently relocate. Instead, because sungazers have a complex social structure (Parusnath, 2020), individuals may have visited neighbouring burrows for reasons that are not yet known (Ruddock, 2000; Stanton-Jones, 2018).

The effects of grazing on grassland reptile species varies with grazing intensity (Masterson et al., 2008; Howland et al., 2014; Neilly et al., 2018; Doherty et al., 2020). A relation of reptile assemblages to different livestock stocking strategies, and therefore grazing intensity, found that when stocking rates are managed sustainably, reptile communities may be unaffected, but the converse was true when stocking rates were high (Neilly et al., 2018). Howland et al.

(2014) also reported that under high grazing regimes, the chances of finding reptiles were low, but also showed that at moderate grazing intensities was related to higher species richness. Previously, the Overgrazed Rangeland site in this study had a high abundance of grazers, which resulted in many parts of the habitat being overgrazed, possibly even severely. This could explain the decline, low burrow fidelity, and movement patterns seen in the *S. giganteus* subpopulation at this site. Similar movement patterns have been reported for *Pedioplanis l. lineoocelata* (Ocellated sand lizard; Wasiolka et al., 2009) that travelled greater distances in highly grazed habitats. There are three possible explanations for this: 1) a lack of food resources in severely overgrazed habitat patches forces the lizards in search of microhabitats more conducive to their foraging demands (Wasiolka et al., 2009); 2) for thermoregulatory reasons (Stanton-Jones et al., 2018); or 3) increased exposure to predation as a result of severe overgrazing may force the lizards to seek alternative refuge sites (Pietrek et al., 2009). It is therefore possible that even though stocking rates at the overgrazed rangeland are much lower than they were prior to this study, the initial effects of previous overgrazing could explain the patterns found in the population demographics, and behaviour of sungazers in this study.

Although habitat transformation is known to generally have a negative impact on reptile populations, the impact caused by mine-altered habitats appears to be particularly severe (Doherty et al., 2020). Mining is known to cause changes to habitat structure, not only through the physical alteration (destruction) of habitats, but also through contaminants in the soil and water (Sasaki et al., 2015). Even though the subpopulations of sungazers were not directly affected by the structural changes in the landscape from the nearby mine, the subpopulations remained in close proximity to the mines. Thus, the lizards were still subjected to mine waste contamination which likely had an impact on the surrounding habitat in which the lizards occupy (Sasaki et al., 2015). Consequently, exposure to these contaminants has caused the sungazers at this site to have higher concentrations of inorganic contaminants in their blood (McIntyre and Whiting, 2012). McIntyre and Whiting (2012) reported a trend that suggested mining contaminants to have an impact on the body condition of sungazers, but the effects on sungazer abundance were inconclusive. Mine contamination has also been linked to reduced reproductive rates in reptiles (Sasaki et al., 2015). This could also explain the reduced abundance of sungazers at the mine-contaminated sites. The findings suggest that the long-term effects of such contaminants could be detrimental to sungazers. However, even though the results of this study have addressed the ecological consequences of

mining contamination to these sungazers, the physiological effects of such contamination over more than a decade remains unknown.

This study is the first to report on decades-long changes in sungazer population demographics at a fine spatial scale. Although it is well known that sungazers are negatively impacted by anthropogenic activities (Van Wyk, 1988; Jacobsen, 1989; Mouton, 2014; Parusnath et al., 2017), how those activities affected sungazer abundance over time was poorly known. This study has provided the first indication of these effects. Parusnath et al. (2017) conducted a broadscale assessment of *S. giganteus* and estimated that the population was two thirds its size 40 years ago, citing habitat fragmentation and illegal harvesting as the primary drivers of local extinctions. Parusnath et al. (2017) also estimated a population decline of 48% since the development of commercial agriculture. Because the results in our study show a decline of more than 50% in three different sungazer subpopulations over a much shorter period, and across different transformed habitats, it is possible that Parusnath et al. (2017) may have overestimated the current size of the sungazer population. Even though this study focused on temporal changes in sungazer population demographics across different transformed habitats, and not on the effects of illegal harvesting, the results suggest that the species may be more vulnerable to the effects of habitat transformation than previously thought.

Habitat transformation caused by mine contamination and severe overgrazing appear to be limiting factors for sungazers. The continued growth of the human population, and unsustainable use of land within *S. giganteus* habitat, are likely to exacerbate the threat that these lizards face. This study has highlighted the importance of regular monitoring of sungazer subpopulations and it is recommended that annual surveys be conducted at all farms that have individually marked sungazers. While some subpopulations of sungazers have gone locally extinct (Parusnath et al., 2017), I emphasise that the remaining subpopulations are also experiencing declines in numbers, especially where land has been transformed.

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CHAPTER 4

Burrow site selection by the Sungazer (*Smaug giganteus*)

ABSTRACT

Elucidating the factors that drive microhabitat selection by a species is important for understanding the species' natural history, and for informing conservation management practice. For species that use microhabitats as long-term or permanent refuge sites, selection pressures must be strong in order for the microhabitat to fulfil their eco-physiological and life history requirements. *Smaug giganteus* (sungazer) is a threatened (Vulnerable) species where individuals seek long-term, often permanent, refuge in self-constructed burrows within the Highveld grasslands of South Africa. This life history trait likely increases their sensitivity to habitat transformation. Thus, knowing the ecological drivers of burrow site selection by sungazers is critical for future conservation management practices. I assessed microhabitat characteristics that may be influencing burrow site selection by sungazers. To do this, I measured vegetation characteristics surrounding sungazer burrows and compared these to vegetation at randomly selected sites, and also recorded burrow orientations and slope aspect. Sungazers appeared to select microhabitats to construct their burrows where vegetation cover was low (median = 10%) and vegetation height was short (median = 21 cm). Seventy-five percent of sungazer burrows orientated in a northerly direction were also situated on north-facing slopes. This suggests that when constructing their burrows, sungazers have a preference for orientating entrances with the aspect of the slope, and generally favour northerly orientations. These findings provide some important information to assist conservation decision makers with designing translocation protocols for the species. I 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 the success rate of the translocation.

Keywords: burrow selection, habitat transformation, grassland, microhabitat, reptile, *Smaug giganteus*, vegetation cover

4.1. Introduction

When animals select habitats or microhabitats in which to live, they do so by taking many factors into consideration. Appropriate selection of habitats and microhabitats may offer improved body condition (Stark et al., 2022), facilitate foraging opportunities (Perry and Garland, 2002; Whitaker and Shine, 2003), influence thermoregulatory behaviours (Huey et al., 1989), provide nesting opportunities (Huey et al., 1989; Kolbe and Janzen, 2002), and may assist with protection against predators (Kacoliris et al., 2010). Careful choice of these factors may be particularly important for ectothermic animals, such as reptiles, whose physiologies are strongly influenced by the environments in which they live (Huey, 1991; Vitt and Cadwell, 2013). Therefore, in many instances there is strong selective pressure on choosing favourable sites to take ambush or to seek refuge, especially for animals that use certain microhabitats as permanent refuge sites. Knowing how these factors drive microhabitat selection is necessary to inform conservation decision making.

Vegetation structure and cover appear to be 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 have a preference for microhabitats with reduced vegetation (Dias and Rocha, 2004). In such instances there are differences in how these microhabitats are used. For example, those living in highly vegetated areas may have reduced activity periods due to limited sunlight availability (Dias and Rocha, 2004). This suggests that the microhabitat needs to offer sufficient eco-physiological support during activity periods. Reduced vegetation cover may promote early visual detection of predators. This 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). When thermoregulation is considered, open microhabitats with short vegetation may provide ideal basking opportunities (Whiting et al., 1993), while increased vegetation cover and certain types of vegetation may offer shaded patches and microclimates to facilitate thermoregulation (Song et al., 2017, Warner, 2023). From a foraging perspective, reduced vegetation cover caused by grazing animals may offer a food resource benefit, as dung left by these animals may attract a high abundance of invertebrates (Atkinson et al., 2004). Thus, while there is much variation in vegetation structure and cover across different landscapes, how those are used is species dependent, and highlights the significance of careful site selection.

Many reptiles seek refuge in burrows which are often interspersed among vegetation within landscapes. Seeking refuge or shelter in burrows not only provides a stable thermal environment, but offers protection against physiological, ecological and environmental extremes. Reptiles may seek temporary refuge in burrows constructed by other animals (e.g., Davidson et al., 2008; Grillet et al., 2010), or by sharing burrows with other animals (e.g. Mulder and Keall, 2001). Some species, however, construct their own burrows and use them as long-term or permanent refuge sites (e.g., Van Wyk, 1992). In such instances, selecting appropriate sites to construct burrows may also be driven by characteristics of the vegetation cover, soil type and soil composition (Jones and Dorr, 2004; Naderi et al., 2011). 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 complex social structures, selection of suitable microhabitats in which to construct burrows may also be influenced by the abundance of these microhabitats within the landscape. Thus, there must be strong selective pressure on 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 (e.g., 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), increase predation risk (Pietrek et al., 2009), influence behavioural patterns (Wasiolka et al., 2009), limit dispersal (Nowakowski et al., 2013), and may alter the population dynamics of a species (Gardner et al., 2009). All these factors can be detrimental to the survival of a species but may be more concerning for habitat specialists and those that are already threatened. For these species, conservation action in the form of protected areas (Gibbons, 2022) or translocation programmes (Van Wyk, 1988; Mouton, 2014; Parusnath, 2014) is necessary to reduce the risk of extinction. However, for translocations to be successful, accurate knowledge on how species are selecting and using habitats and microhabitats is required.

The sungazer (*Smaug giganteus*) is a threatened (Vulnerable; IUCN, 2022), heavily-armoured lizard that is endemic to the Highveld grasslands of South Africa (De Waal, 1978; Jacobsen, et al., 1989; Van Wyk, 1992). These long-lived, large-bodied lizards are unlike most other species in the Cordylidae in that they use self-constructed burrows in the grassland mosaic as long-term, often permanent, refuges (Van Wyk, 1992). Activity is also centred in close proximity to the home burrow (Van Wyk, 1992; Ruddock, 2000; Stanton-Jones, 2018). This philopatric nature suggests that sungazers are carefully selecting microhabitats in which to construct their burrows. However, since the Highveld grasslands support extensive agricultural activities (DEAT, 2005), and mining activities (McIntyre, 2006), sungazer subpopulations are susceptible to decline because of habitat transformation and fragmentation (Van Wyk, 1992; McIntyre and Whiting, 2012; Parusnath, 2014). Thus, accurate knowledge on how sungazers are selecting microhabitats in which to construct their burrows is necessary to inform future translocation protocols, especially considering that previous translocation attempts have been unsuccessful (Groenewald, 1992; Parusnath, 2014).

In this study, I identified some of the factors that drive burrow site selection within the grassland matrix by sungazers, and recorded some important burrow metrics. I compared microhabitat characteristics around each burrow to nearby random sites available in the surrounding landscape. Because of anecdotal evidence from field observations, and because sungazers exist in an agricultural landscape where the abundance of grazing animals can be high, I 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 that burrows would face in northerly directions. Accurate knowledge of factors influencing burrow site selection in sungazers may not only facilitate future surveys, but provides further knowledge for conservation management plans for this vulnerable species.

4.2. Methods

4.2.1. Study site

This study was conducted between November 2019 and December 2022. I visited 24 privately-owned farms across the eastern, central, and western regions of *S. giganteus* distribution within the Free State Province, South Africa. Specifically, these farms 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 often located (Fig. 4.1). Given the threatened status of the species, I have omitted precise locational data on recommendation of the South African National Biodiversity Institute (SANBI, 2022).

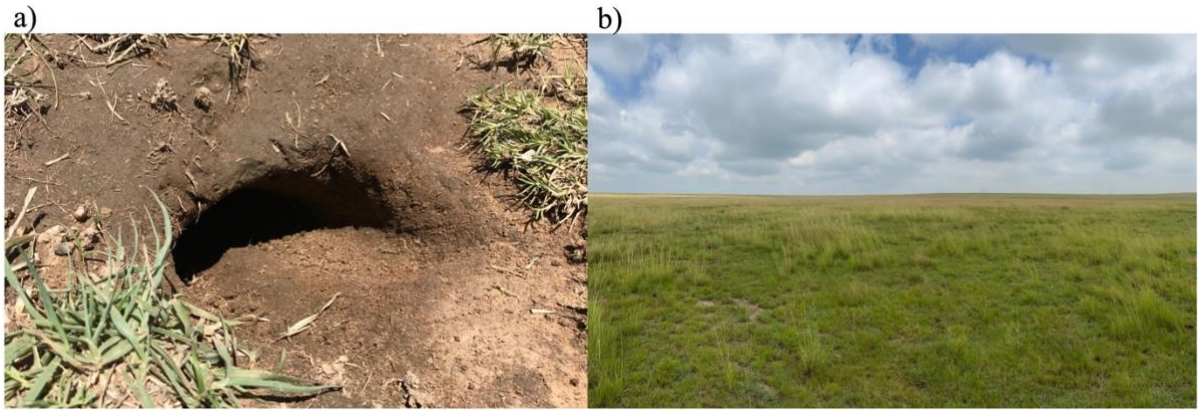


Figure 4.1: An active sungazer burrow (a) and grassland mosaic (b) showing bare open patches amongst denser areas of vegetation.

4.2.2. Experimental design and protocol

4.2.2.1. Field sampling

I located 106 sungazer burrows across 24 different sungazer colonies. Although I attempted to locate at least five sungazer burrows from each colony, on occasion, a minimum of two burrows were located due to the low abundance of sungazers on the property. Sungazer burrows are identifiable by their kidney-shaped entrance, and bare patch leading towards entrances (Van Wyk, 1992). To assist with locating sungazer burrows, I used records from previous studies (e.g. McIntyre, 2006; Parusnath, 2014; Stanton-Jones, 2018). At sites where previous records of sungazer burrows were unavailable, I walked line transects, 5 m apart, to find previously unrecorded sungazer burrows (Parusnath et al., 2017), and 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, I 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) estimated percentage of vegetation cover greater than 10 cm in height (vegetation cover); (4) mean height of vegetation, (5) number of animal droppings (excluding droppings from sungazers), and (6) number of animal

burrows (excluding sungazer burrows). For the mean height of vegetation, I took three measurements at different points within the quadrat and used these values to calculate a mean score. I also recorded if burrows were occupied by inspecting if burrow entrances were clean from debris, if sungazer scales were present, if claw or tail markings at entrances were present, or in several instances by inserting a Bosch borescope camera (Bosch GIC 120 C) down burrows. To assess whether sungazers choose to construct their burrows within specific microhabitats within the grassland mosaic, I recorded the same attributes within an equal number of 4 m^2 quadrats at random locations. Random points were located by spinning a pencil at confirmed sungazer burrows where attributes were measured, and letting it fall to the ground to determine the direction to the random point. A random number generator was then used to produce a number between 10 and 100, and I walked the resulting number of paces in the direction indicated by the pencil.

4.2.2.2. Soil parameters

Since sungazers may use self-constructed burrows as permanent refuge sites (Van Wyk, 1992), the composition of soil may affect where burrows are constructed. Thus, the coordinates of each study site were overlayed onto the 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. I then extracted and recorded the components of soil composition (% sand, % silt, and % clay) associated with each study site. It is, however, important to note that these are broadscale measures, and not necessarily the exact measures associated with sungazer burrows. Therefore, these broadscale measures also represent the random sites in this study. Nevertheless, these measures give an indication of the range of each soil parameter associated with sites in which sungazers occur.

4.2.3. Statistical analyses

All statistical analyses were performed in *R* 4.1.1 (R Core Team, 2021).

4.2.3.1. Soil parameters

Since only a single measure of each soil parameter was available for each study site, variance within each site could not be measured. Thus, only descriptive statistics across study sites for the different soil parameters are presented. However, the non-parametric Kruskal-Wallis test was conducted to test for differences between soil parameters (sand, silt, and clay). This was

chosen as the assumptions of normality were not met, even after the arcsine square root transformation was applied. Dunn's test with a Bonferroni adjustment was used for post-hoc analyses between soil components.

4.2.3.2. 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. The remaining microhabitat characteristics associated with sungazer burrows and random sites were tested for normality using the Shapiro-Wilk test. None of the variables met the assumptions of normality even after the appropriate transformations were applied (arcsine square root transformation for proportion estimates, and log transformations for the remaining variables). Thus, since this study followed a paired design, I used Wilcoxon signed-rank tests 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). Because non-parametric tests were used, the median values for microhabitat characteristics are reported.

4.3. Results

4.3.1. Soil parameters

Soil parameters of sand, silt and clay content were statistically different from each other (X^2 = 38.69, df = 2; $p < 0.05$). Sand content was highest ($\bar{x}$ ± SD = 56.9 ± 17.0%; $p < 0.05$), followed by clay ($\bar{x}$ ± SD = 23.4 ± 13.6%), and silt ($\bar{x}$ ± SD = 19.3 ± 4.2%) content (Fig 4.2). However, there appeared to be no statistical difference between clay and silt content ($p >$ 0.05), but clay content had a wider range compared to silt content (Fig 4.2).

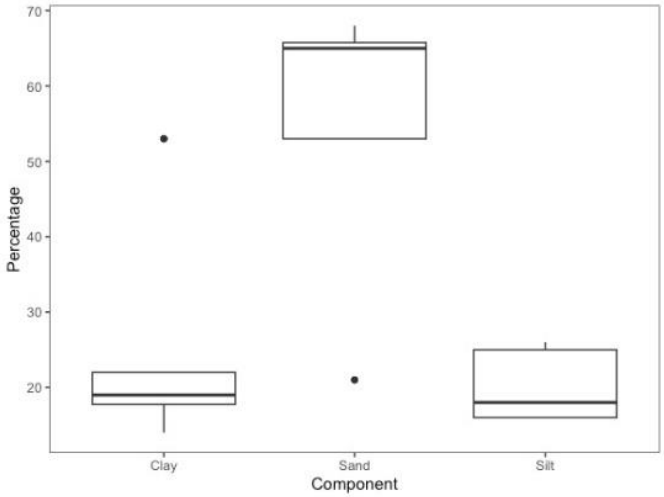


Figure 4.2. Soil parameter estimates (%) of clay, sand, and silt content at farms in which sungazers occur. Due to the broadscale nature of the soil composition GIS layer, random sites also fall within these estimates. Black circles depict outliers in the dataset.

4.3.2. Site attributes

4.3.2.1. Burrow orientation and land aspect

Of the 106 recorded sungazer burrows, nearly 60% of entrances were north, north-east, or north-west facing (northerly orientations). Comparatively, less than 30% of sungazer burrows had entrances facing south, south-east, and south-west (southerly orientations). A significant association between the orientation of burrow entrances and land aspect existed (X^2 = 106.97, df = 56, $p < 0.05$) with most burrows orientated in northerly directions being situated on north facing slopes (75%; Fig. 4.3). Although burrows that are not orientated in northerly directions appear to be randomly distributed across different slopes, 50% of southerly orientated burrows also occurred on south facing slopes (Fig 4.3).

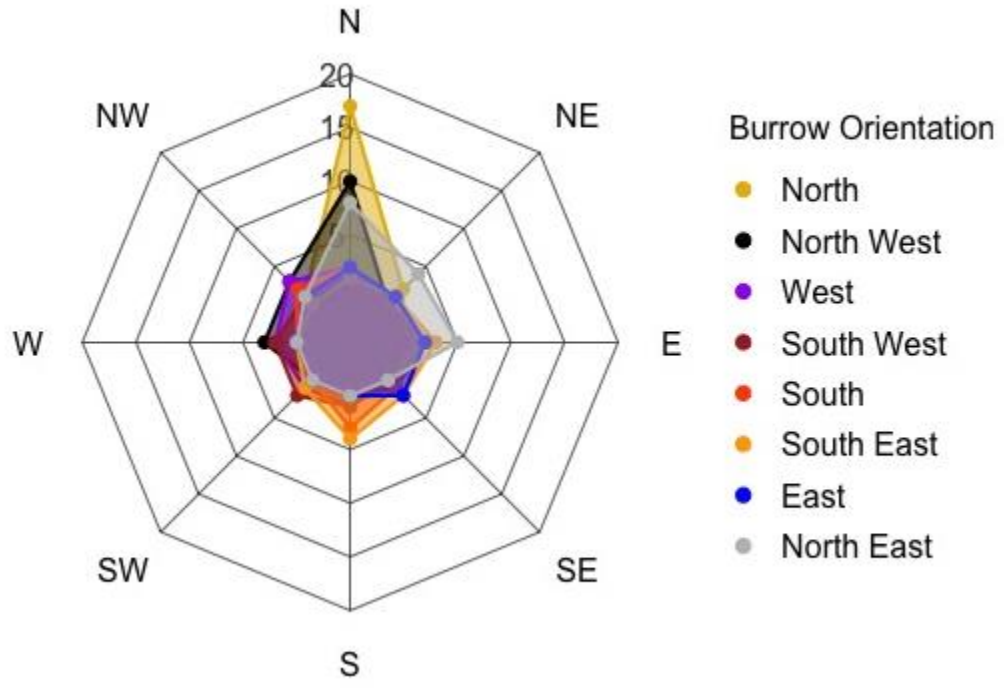


Figure 4.3. The number of sungazer burrows and the orientation of their entrances in relation to the aspect of the land slope. The chart represents the slope aspect while the points depict the orientation of burrows at the slope aspect. Aspect and burrow orientations were assigned according to compass directions.

4.3.2.2. Microhabitat characteristics

Percent vegetation cover was significantly less at sungazer burrows compared to paired random sites (V = 237, $p < 0.05$), with a median value for vegetation cover at burrows and random sites of 10% and 70%, respectively (Fig. 4.4). Sungazer burrows were also associated with significantly shorter vegetation compared to random sites (V = 596, $p < 0.05$). The median height of vegetation at sungazer burrows was 21 cm compared to 30.5 cm at random sites (Fig. 4.5). Of the 106 paired samples, only five sungazer burrows had a maximum of two other animal burrows within the measured quadrat, and three random sites had only single animal burrows. No significant difference existed between these measures (V = 28.5, $p = 0.15$). There was also 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 (Fig. 4.6).

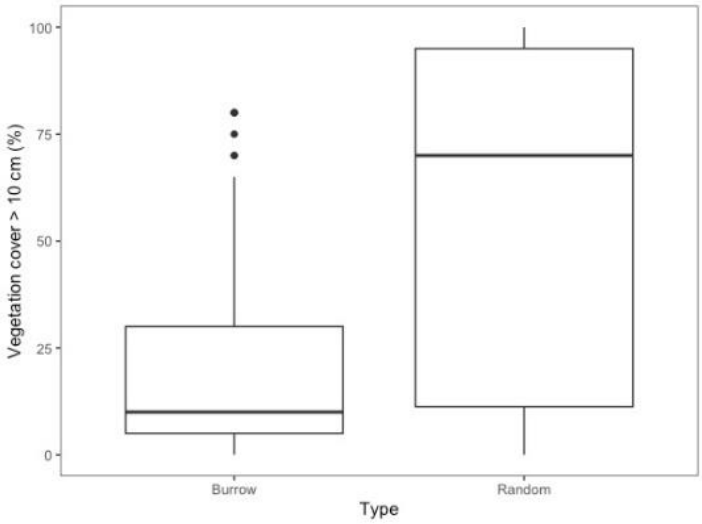


Figure 4.4. A comparison of vegetation cover (> 10 cm vegetation height) within 4 m^2 quadrats of sungazer burrows (n = 106) and random sites (n = 106). Black circles depict outliers in the dataset.

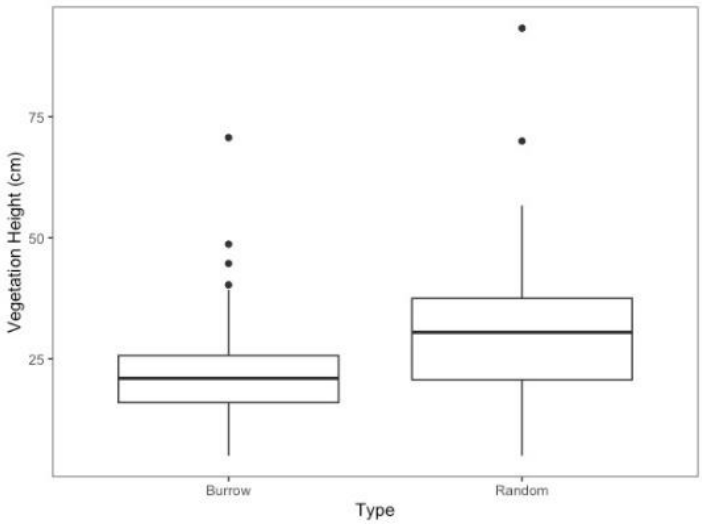


Figure 4.5. A comparison between the height of the vegetation within 4 m^2 quadrats of sungazer burrows (n = 106) and random sites (n = 106). Black circles depict outliers in the dataset.

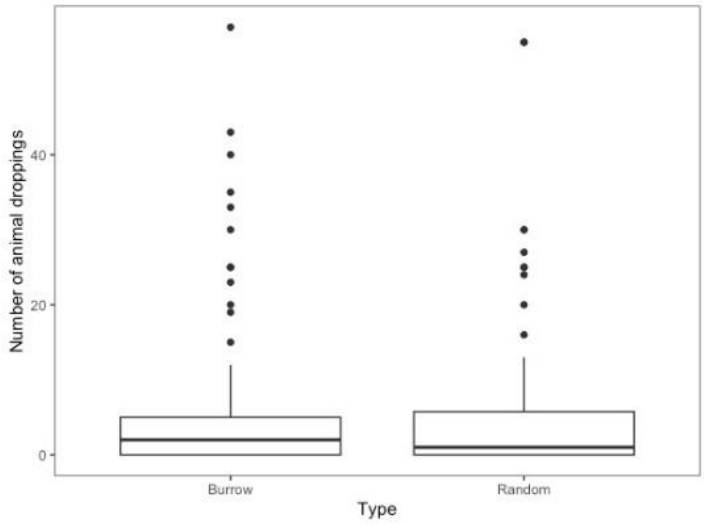


Figure 4.6. A comparison between the number of animal droppings within 4 m^2 quadrats of sungazer burrows (n = 106) and random sites (n = 106). Black circles depict outliers in the dataset.

4.4. Discussion

I assessed the microhabitat characteristics that may influence where sungazers choose to construct their burrows. In general, sungazers exist in a landscape where sand is the main component of soils, but soils also consist of a mixture of clay and silt. Sungazer appear to be selecting specific microhabitats in which to construct their burrows, with burrows existing in patches within the landscape characterised by low vegetation cover, and short vegetation. By comparison, random sites within the landscape are associated with high vegetation cover with tall and dense grasses. When constructing their burrows, sungazers have a preference for orientating burrow entrances according to the aspect of the slope, and select north facing slopes on which most burrow entrances face in northerly directions. Although only a limited number of attributes of sungazer burrows and microhabitat characteristics were assessed in this study, the findings reveal that there is clear selection for particular microhabitats for burrow sites which provides valuable information to future translocation protocols.

Sungazers exist in a landscape with relatively high sand content in the soil. Although, this finding was based on a broadscale assessment of soil parameters within regions where sungazers occur, and is not specifically associated with sungazer burrows, it suggests that sandy soils are an important factor for sungazer burrows. This is likely because sandy soils may promote good drainage, and may support burrow construction (e.g., Landers and Speake, 1980; Jones and Dorr, 2004). Soils within the landscape are also composed of a mixture of

clay and silt. Because sungazers may seek permanent refuge in their burrows, it is possible that higher clay content may offer long-term structural benefits to their burrows. However, the exact soil parameters associated with sungazer burrows remains unclear, but it seems that soil composition may also be a driving factor for burrow site selection (see Chapter 2).

Most sungazer burrows were found in regions of the landscape with little vegetation cover, supporting my initial predictions. This suggests that sungazers are selecting fairly open areas to construct their burrows where grasses and vegetation are short. This may be because of the eco-physiological advantages that these microhabitats may offer. Because sungazers thermoregulate near their burrows by adjusting body posture and orientation (Stanton-Jones et al., 2018), dense vegetation and increased cover may reduce sunlight at the surface, affecting their ability to thermoregulate effectively. Thus, reduced vegetation cover may facilitate behavioural thermoregulation in sungazers by increasing access to direct sunlight. From an ecological perspective, the ability to detect predators may be limited in highly vegetated habitats. Therefore, having their burrows situated in habitat patches with reduced vegetation cover may assist sungazers in escaping predation since predators cannot approach unobserved. Low vegetation cover may also enhance prey detection and acquisition. These advantages may be particularly important for sungazers given their sedentary lifestyle (Van Wyk, 1992; Ruddock, 2000; Stanton-Jones, 2018).

In general, sungazers appear to have a preference for selecting northerly facing slopes on which to construct their burrows. This is not surprising since these slopes are associated with increased levels of direct solar radiation (Barton et al., 2019), and may therefore facilitate thermoregulation in sungazers (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. Anecdotal evidence from field observations 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 test this hypothesis. Thus, there appears to be physiological and ecological benefits to sungazers by having their burrows orientated with slope aspect.

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 grazers within sungazer habitat, I expected sungazers to select sites where grazing frequently occurs as dung left by grazing ungulates may attract a high abundance of invertebrates (Atkinson et al., 2004), providing sungazers with a food resource benefit. However, while this may be plausible in landscapes where game occurred 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, in which only a fraction of sungazer subpopulations occur. Thus, while dung may provide a food resource benefit to 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 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 could be made, contributing to our knowledge of the factors that may influence burrow site selection by sungazers. However, there were a few limitations. Even though this study has provided an indication of the soil parameters associated with farms on which sungazers occur, no direct link between soil composition and sungazer burrows can be made. 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 at farms with a high abundance of grazers, they still have statistical implications, and therefore I caution against overinterpretation of those findings. In addition, my study focused on the vegetation density surrounding sungazer burrows, and while the findings are valuable for the future conservation of the species, the species composition of the grasses surrounding sungazer burrows may also be important. Despite some limitations, this study has revealed some of the driving factors behind burrow site selection by sungazers, and has recognized the need for further studies on habitat preference of the species.

Although sungazers seem to have a preference for selecting microhabitats with reduced vegetation cover, some reptile species tend to prefer habitats where vegetation cover is high. For example, Masterson et al. (2009) reported increased species richness in grasslands when vegetation cover increased. This is likely because increased vegetation cover is related to

improved body condition (Stark et al., 2022), offers thermoregulatory benefits (Bauwens et al., 1999), and can offer protection against predation (Pietrek et al., 2009). However, sungazers are philopatric lizards that rarely stray further than 2 m from their burrow entrances (Van Wyk, 1992; Ruddock, 2000; Stanton-Jones, 2018). Because burrows are often associated with open bare patches of ground leading up to entrances, these patches may retain heat for longer (e.g., Whiting et al., 1993) than if densely vegetated, offering more thermoregulatory options. Even though postural and orientation adjustments are primary behavioural thermoregulatory techniques (Stanton-Jones et al., 2018), by maintaining activity close to burrows, shuttling behaviours in and out of burrows may also facilitate thermoregulation, negating the need for cover offered by highly vegetated habitat patches. Similarly, not only do open microhabitats promote early detection of predators, but burrows offer sungazers permanent refuge sites and remaining close to them facilitates rapid escape from predation. Thus, because of their life history traits, sungazers are still able to receive similar benefits in open microhabitats with reduced vegetation cover as species living in densely vegetated areas.

The factors driving interspersed patches of microhabitats with reduced vegetation cover goes beyond the scope of this study. However, it is likely that these areas consist 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. 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. While the high number of sungazers at this site suggests a possible symbiotic relationship between sungazers and grazing animals, severe overgrazing may be detrimental to the survival of sungazer subpopulations in habitats where grazing is high (see Chapter 3). Thus, although sungazers may benefit from the microhabitats caused by grazing animals, I caution landowners against overgrazing livestock in areas occupied by sungazers, and recommend careful management of rotational grazing regimes.

Preference for orientating burrow entrances towards a particular direction appears to be species dependent. For example, *Liopholis inornata* (desert skink) has a preference for orientating the entrances of their burrows in northerly directions (Pianka and Giles, 1982), which was similar to what was found in sungazers. Another species, *Liopholis striata* (night skink) favoured southerly directions in which to orientate their burrows (Pianka and Giles, 1982), which although not the norm for sungazers in this study, was similar to a few of the

burrows recorded. Pianka and Giles (1982) suggested that preference for a particular orientation appears to be driven by thermoregulatory demands. This also seems to be the case in sungazers given the strong association between the aspect of the slope and burrow orientation. By contrast, Fenner et al. (2012) found no preference for a particular orientation of burrow entrances in *Liopholis slateri* (Slater's desert skink). However, 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.

Habitat transformation within sungazer distribution is common and is one of the primary threats that these lizards face (Parusnath, 2014). Consequently, translocation of sungazer subpopulations from areas where developments are planned are often necessary to reduce the species risk of extinction. However, previous translocation attempts of some subpopulations 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). This study attempted to address a few of the factors that may influence where sungazers choose to construct their burrows, and therefore has direct conservation benefit by contributing to the development of translocation protocols. Thus, although detailed knowledge of the soil composition associated with sungazers is still required to enhance translocation protocols, I recommend that natural grasslands, and habitat patches with reduced vegetation cover interspersed amongst densely vegetated areas are included in these protocols. When constructing artificial sungazer burrows, entrances should also match the aspect of the slope.

The assessment of several simple habitat characteristics associated with sungazer burrows has provided insights into the factors that contribute to burrow site selection by sungazers, as well as some important burrow attributes. Although this study may enhance translocation protocols, I caution conservation authorities against rapid implementation. Instead, I recommend soft-release translocation attempts on smaller subpopulations of sungazers (if possible), and that careful, continuous monitoring programmes follow to identify the success rate.

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CHAPTER 5

Synthesis, limitations, recommendations for conservation, and conclusion

5.1. Synthesis

Some of the primary challenges that animals experience as a consequence of selecting habits in which to live include the threat of climate change (Sinervo et al., 2010), and habitat transformation (Keinath et al., 2017). Some species, however, may be more susceptible to these threats because of their life history traits, restricted geographic ranges, or because of a combination of these factors. The sungazer (*Smaug giganteus*), is an example of a species that has a restricted geographic range, and life history traits that are likely to increase their risk of extinction due to the combined effect of climate change and habitat transformation. In this thesis, I aimed to assess the consequences of habitat selection by sungazers in a changing world. Although this study focused on a single species, and there were many limitations, the findings provide important information that applies, not only to sungazers and their conservation, but to other species exhibiting similar traits.

Although there are many ecological factors that influence where reptiles choose to live, at the broadscale level, climate may arguably be one of the most influential. However, it also means that climate change is a major threat that many reptile species face (Sinervo et al., 2010; Böhm et al., 2016) and coping with it is challenging. Possible responses to climate change include: 1) behavioural compensation, 2) evolutionary adaptation, 3) range shifts and expansions or contractions, or 4) extinction (Bradshaw and Holzapfel, 2006; Sinervo et al., 2010; Böhm et al., 2016). However, predicting how a species may respond to climate change requires accurate knowledge of species life history traits, dispersal capacity, habitat requirements, and factors limiting geographic distribution. For many species, data for some or all these factors are limited. Nevertheless, because of the impact of climate, and because evolutionary adaptation would require long time periods (Bradshaw and Holzapfel, 2006; Sinervo et al., 2010), a common response to climate change for reptiles is to shift their distribution by tracking suitable climates (e.g., Moreno-Rueda et al., 2012; Petford and Alexander, 2021).

One of the first steps in assessing a species vulnerability to climate change is to model its ecological niche envelope. Although there are several modelling techniques, correlative

ecological niche models (ENMs), such as the maximum entropy (Maxent) method, are commonly used (e.g., Houniet et al., 2009; Petford and Alexander, 2021), especially because behavioural and physiological data for many species are lacking. By using ecologically relevant bioclimatic and environmental variables that are associated with the species distribution, these models can produce predictions with improved accuracy (Anderson and Gonzalez Jr., 2011; Guevara et al., 2018). Similarly, as shown in Chapter 2 and supported by Anderson and Raza (2010), it is important to use an appropriate scale (such as the buffered extent in Chapter 2) to model a species geographic range as this may facilitate predictions relating to shifts in a species distribution when models are projected into the future. However, given the complexities associated with modelling species distributions and making predictions about their future suggests that model predictions need to be interpreted with caution. As in Chapter 2, interpretation of model predictions can be enhanced when life history traits and the exposure to extrinsic factors (e.g., habitat transformation) of a species are considered. Though these factors may not always be available and are not necessarily easy to incorporate into the modelling algorithm, information that is known can still be applied post-prediction.

In Chapter 2, I modelled the ecological niche envelope of sungazers and projected the models into the future under two climate change scenarios. The models predicted negligible change for sungazer distribution under the moderate case scenario, but a higher vulnerability to climate change under the worst-case scenario. In both scenarios the species was predicted to shift their geographic range to the southwest. For generalist species, and those with high vagility, the ability to shift their geographic range may be increased (Clavel et al., 2011), assuming that geographic barriers do not limit dispersal. The sungazer is, however, a habitat specialist, whose life history traits (e.g., low fecundity and dispersal ability; Van Wyk, 1992; Stanton-Jones, 2018), strict microhabitat requirements (Chapter 4), and fragmented habitat may not only hinder its ability to track suitable climates, but are also likely to affect other responses such as evolutionary adaptation. Thus, sungazers are probably more vulnerable to the effects of climate change than what was initially predicted. These results not only suggest that habitat specialists may be more vulnerable to climate change than what correlative models may predict, but also suggests that the predictions made by these models may not be definitive. Nevertheless, they do give an indication about the vulnerability of a species to climate change.

The geographic range of sungazers falls over an agriculturally important region of South Africa (DEAT, 2005). Thus, it is no surprise that one of the primary threats that sungazers face is habitat transformation. In Chapter 3, I provided the first fine-scale assessment of the potential effects of habitat transformation on sungazer subpopulations. Despite the availability of only a few sites for assessment, it is clear that sungazers are more vulnerable to effects of habitat transformation than previously assumed (e.g., see Parusnath et al., 2017), irrespective of how the land is transformed. An expansion of the human population in the future will likely increase the need for more agricultural activities which would further fragment sungazer habitat. Similarly, because much of the landscape within sungazer distribution is suitable for solar farms (Fluri, 2009; Singh, 2016), if the demand for these farms increases and they become more abundant, it may result in the local extinction of many sungazer subpopulations. Thus, when combining the threat of habitat transformation and fragmentation to the pressures of climate change, sungazers could face extinction, or at the very least, many subpopulations would become locally extinct. Therefore, conservation management for the species is critical.

To further enhance conservation management of a species, it is important to know the habitat requirements of the species, and how it is using the habitat. This may be particularly true for habitat specialists, and species that seek permanent refuge in crevices or burrows. Since sungazers seek permanent refuge in self-constructed burrows (Van Wyk, 1992), and can use the same burrow for their entire life (see Chapter 3), it is no surprise that individuals are carefully selecting suitable microhabitats in which to construct their burrows. In Chapter 4, I assessed the factors that could be driving microhabitat selection by sungazers. Sungazers are unlike many other reptile species in that they select microhabitats associated with low vegetation cover where grass height is also significantly shorter than in the surrounding landscape to construct their burrows. These microhabitats are generally selected on northerly facing slopes on which sungazers also orientate the entrances of their burrows in a northerly direction. Although it is unclear why sungazers are selecting these habitats, it is likely that such microhabitats facilitate thermoregulation, and offer early visual detection of potential predations. These benefits would be important for a philopatric species such as the sungazer that rarely moves further than 2 m from their burrow entrance (Van Wyk, 1992; Ruddock, 2000; Stanton-Jones, 2018).

Many species are vulnerable to the effects of climate change and habitat transformation. Although this thesis focused on a single species, the potential impact that the findings will have on conservation management for sungazers, and species exhibiting similar traits, are important. The findings in this thesis should highlight the severity of the impact of climate change and habitat transformation not only on sungazers but to other species too, especially to habitat specialists, those with limited dispersal capacity, and those with restricted geographic ranges. Climate change and habitat transformation are serious threats on their own, but when combined, the threat of extinction for species already considered threatened is exacerbated.

5.2. Limitations and future directions

This thesis provided novel information on *S. giganteus*, and crucial data to inform conservation management of the species. However, as is common in scientific studies, there were limitations in this research that reveal the need for further research on sungazers:

5.2.1. Vulnerability to climate change

Sungazer vulnerability to climate change may be impacted by changes in land use. Due to uncertainties associated with making predictions about future land use, and the lack of detailed anthropogenic development (e.g., human population density, road, and railway densities) GIS layers over sungazer distribution, I could not incorporate these factors into my models. While I used knowledge about land cover and anthropogenic activities currently existing in sungazer habitat to enhance my interpretation of the model predictions, I suspect that predictions on sungazer vulnerability to climate change will be significantly increased if accurate estimates of future land use change and anthropogenic developments over sungazer distribution are incorporated into the modelling algorithms. Nevertheless, Chapter 2 has provided the first indication of how sungazers could be affected by climate change in the future.

5.2.2. Habitat transformation

In Chapter 3, I provided the first fine-scale assessment of the potential impact that habitat transformation has on sungazer subpopulations. Unfortunately, however, my sample size for sites was necessarily limited; only four study sites existed where almost all individual sungazers from the entire subpopulations were permanently marked with Passive Integrated Transponders (PITs; McIntyre, 2006). If most individuals from more sungazer

subpopulations across different habitat types were marked with PITs, and monitored annually, not only would this lead to more informative assessments about population turnover and dynamics of sungazers, but would also ensure early detection of potential subpopulation declines resulting from anthropogenic activities and could lead to swift conservation action being taken to mitigate the effects.

5.2.3. Microhabitat selection

Although I reported in Chapter 4 on the range of soil parameters that could be available for sungazers, the focus was at the broadscale level. Because sungazers may use their self-constructed burrows during their entire life (see Chapter 3), it is likely that fine-scale differences in soil composition between sungazer burrows and the surrounding landscape could exist. An assessment of these differences would contribute to the findings in Chapter 4 on microhabitat selection by sungazers and would further enhance translocation protocols for the species. In addition, an assessment of environmental temperatures near sungazer burrows and near random sites within the landscape would provide an indication of the microclimate selected by sungazers.

5.3. Recommendations for conservation

Parusnath et al. (2017) argued that the primary cause of decline in the sungazer population was likely due to a combination of threats; poaching, and habitat transformation and habitat fragmentation. However, the findings by Parusnath et al. (2017) and Parusnath (2020) have likely resulted in the rate of illegal harvesting of the species for the pet trade being reduced. This means that the effects of habitat transformation and fragmentation remain a major threat to the species. The findings in Chapter 3 have identified the potential severity of this threat, and in Chapter 2, have identified another major threat to the species; climate change. This suggests that in order to minimize the loss of further sungazer subpopulations, conservation management is crucial.

One of the biggest challenges to the conservation of sungazers is that translocation protocols have been ineffective (Groenewald, 1992; Parusnath, 2017). This is likely due to the lack of knowledge around microhabitat selection by sungazers, and inappropriately constructed artificial burrows. Since the Highveld grasslands are continuously being transformed, effective translocation protocols are necessary to assist in the conservation of sungazers. Below, I use the findings from this thesis to provide recommendations for future protocols:

5.3.1. Broadscale site selection

Given the unlikely scenario that sungazers will shift their distribution to track suitable conditions in the future, emphasis should be placed on developing conservation protocols within the species current interpreted distribution. In Chapter 2, my models predicted that the eastern, south-eastern, and western regions of the species current distribution would become less suitable under future climate change. Since conservation agencies, such as the Endangered Wildlife Trust (EWT), are attempting to establish protected areas for the species (Gibbons, 2022), I recommend that northern, central, southern, and south-western parts are prioritised. Similarly, these areas should also be surveyed to identify possible locations for translocation attempts. It is important to note, however, that landowner involvement is crucial, not only to gain access to survey suitable translocation sites but should an area on a farm be identified as a suitable translocation site, landowners could assist with facilitating translocations and may be able to report on the success rate of the translocated aggregation. Parts of the current sungazer distribution that are predicted to experience contraction in the future should not be ignored. Instead, I recommend continuous monitoring of the subpopulations of sungazers in these regions, and that the 'Sungazer Custodianship Programme' (landowner involvement) developed by EWT continues throughout the species distribution. This would ensure that the habitat of sungazers remains protected, and that potential threats are identified and reported on swiftly such that conservation action can be taken.

5.3.2. Microhabitat selection

Sungazers select microhabitats within the *Themeda trianda* grassland that are associated with low vegetation cover and short grass patches interspersed among densely vegetated regions within the landscape. The response curves in Chapter 2 (and the findings in Chapter 4) indicated that the probability of sungazer occurrence increases in parts of the landscape where sand and clay are the main components of soil. When surveying sites for possible sungazer translocations, I recommend that all these factors are taken into consideration. Ideally, these microhabitats should be situated on slopes facing north, north-east, or north-west. Should suitable microhabitats be located, I recommend that artificial burrow construction follows individual-specific burrow characteristics. If this not possible, artificial burrow construction should follow the general characteristics of sungazer burrows described

by Van Wyk (1992), and that entrances are positioned in the same orientation to which the slope faces (northerly directions).

5.3.3. Soft-release and continuous monitoring

Due to previously ineffective translocation attempts of sungazer subpopulations, I caution against rapid implementation of the recommendations set out in this thesis. Instead, I recommend that translocation attempts follow a soft-release protocol and are trialled on either small subpopulations of sungazers, or small aggregations. An outdoor, fenced-off enclosure should be installed in suitable microhabitats for the translocation attempt. This would allow translocated individuals an opportunity to acclimate and become familiar with their new environment and their artificial burrows (Tuberville et al., 2005; Attum and Rabia, 2016), and would likely reduce predation by ensuring that the translocated individuals do not immediately disperse from the release site. In addition, these enclosures may facilitate the construction of natural burrows if the artificial burrows are rejected by translocated individuals. Similarly, when releasing individuals into these artificial burrows, it is important that all individuals removed from a single natural burrow are released together into the same artificial burrow. All individuals should be permanently marked with PITs before release, and continuously monitored either actively through regular surveys, or passively using the Automated Cellular PIT tag Reader System developed by Stanton-Jones (2018), to identify stability within translocated aggregations and subpopulations. Once the translocated aggregations or subpopulations have become accustomed to their new environment, the enclosure fencing may be removed. However, given the low fecundity in sungazers, it is likely that results on successful translocations would take several years to become available, and therefore continuous monitoring of the translocated aggregation or subpopulation is critical.

5.4. Conclusion

Over the last few decades, research on the sungazer has gained momentum, providing invaluable contributions to the knowledge base of the species. In spite of this, there are many research topics on sungazers that are yet to be explored. Prior to this thesis, not only was knowledge on the microhabitat requirements of sungazers lacking, but the severity of the threats that these iconic lizards face was not well recognised. By modelling the predicted future distribution of sungazers, I have identified climate change as another significant threat, especially when the species life history traits are considered. In addition, I have highlighted

the severity of threat that habitat transformation has on sungazers. By considering the threats associated with the species, it is possible that the current the size of the sungazer population is probably an overestimate. The outcomes of this study have highlighted the importance of swift conservation action, and the hope is that the findings and recommendations contained in this thesis enhance conservation management programmes.

5.5. References

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