Snake community structure in a heterogeneous fynbos ecosystem

Bryan Nathan Cloete

University of the Western Cape, Department of Biodiversity, and Conservation Biology, Private, bag X 17, Bellville, 7535, South Africa.

A thesis submitted in fulfilment of the requirements for the degree of *Magister Scientiae* in the Department of Biodiversity and Conservation Biology, Faculty of Science, University of the Western Cape

Supervisor: Dr. Bryan Maritz

August 2022

Declaration

I declare that "**Snake community structure in a heterogeneous fynbos ecosystem**" is my own work, that it has not been submitted for any degree or examination at any university, and that all sources I have used or quoted have been indicated and acknowledged by complete references.

Full name: Bryan Nathan Cloete   **Date:** August 2022

Signature: ……………………….

UNIVERSITY *of the*
WESTERN CAPE

Abstract

Snake community structure in a heterogeneous fynbos ecosystem

B.N Cloete

MSc. Thesis, Department of Biodiversity and Conservation Biology, University of the Western Cape.

Snakes occur in most terrestrial ecosystems, forming an integral part of many ecological communities. A diverse community of snakes in an ecosystem can indicate a complex habitat structure capable of supporting a diverse assemblage of faunal species. I utilised multiple non-invasive and non-lethal trapping methods to quantify diversity metrics for the snake community occurring in a heterogeneous fynbos ecosystem within the Koeberg Private Nature Reserve (KPNR) over one-year period. Additionally, I sampled the species richness and abundance of snake predators and prey within the reserve and tested the hypothesis that the snake community was impacted by the abundance and diversity of snake predators and prey. I performed several statistical analyses to identify the factors that influence the snake community structure observed in KPNR. One year of sampling resulted in 156 individual snake detections representing ten species. The explanatory variables that typically correlate well with metrics of snake diversity were weak predictors at my study site. Vegetation type, which should have been a reliable predictor for snake habitat use was generally one of the poorest predictors. Thus, the ecological roles of individual species of snakes and the structure of the snake community in KPNR remain unclear. Further studies incorporating both species-specific and environmental variables could hold better insight into the processes that structure the snake community within KPNR. Ultimately, the knowledge gained from this study provides invaluable information on the factors that shape the snake community within KPNR, and indicates a far more complex and diverse community than previously thought.

Acknowledgements

First and foremost, I would like to express my endless gratitude to Dr. Bryan Maritz for allowing me to pursue my postgraduate degree in the Maritz lab at the University of the Western Cape. You were always willing to take the time to provide helpful edits and suggestions for my thesis and your input was invaluable throughout my Masters.

A special thanks to Jurina le Roux and her team at Koeberg Private Nature Reserve for their effort and assistance throughout my sampling.

I would like to thank my colleagues from the Maritz snake lab for your contributions and support. Each of you has provided me with invaluable knowledge that contributed to the completion of my thesis.

To my colleagues and fieldwork assistants who helped me with fieldwork; Silindokuhle Tokota, Tim Ponton, Riaaz Mohammad and Matthew Arendse – Long hours and hard work in the field were made better with each unique banter.

Most importantly, I would like to thank my family. To my parents, Mark and Venessa, for your belief and support, I will be forever grateful for everything you have done for me throughout my life. To my eldest brother, Stephen, your steadfast resolve and perseverance have always been something I can aspire to. To my 'baby brother', Dylan, for your constant motivation, interest in my work and support thank you for everything.

Ethics clearance for research protocols was received from the University of the Western Cape (ref. no. AR 19/7/7).

Contents

List of Tables

UNIVERSITY *of the*
WESTERN CAPE

List of figures

List of Appendices

Chapter 1: Introduction and literature review

We live in an age in which the development of our species comes at the cost of our environment. Over the last century, humanity has changed the environment so rapidly and extensively that most of the world's ecosystems have degraded (Millennium Ecosystem Assessment 2005). While these developments have generated many benefits for our species, they have been devastating to our environment (Morris and Kingston 2002; Mehring et al. 2017). Understanding the resultant decline in biodiversity is a complex task, with challenges arising in assigning responsibility for species loss with correlated causes (Morris and Kingston 2002; Giam 2017). However, there is a significant gap in data pertaining to the ecological impact on ecosystems from the loss in biodiversity, particularly when considering baseline data of community structure (Morris and Kingston 2002; Collen et al. 2008; Ramadoss 2010). To address these challenges, a greater understanding of the factors responsible for shaping ecological communities is required, with emphasis on the role of trophic interactions (Rosenzweig and Winakur 1969; Rainsford et al. 2020). This type of information will allow us to be better informed on how ecological communities function, how to manage them, and how to better conserve biodiversity (Morris and Kingston 2002; Tulloch et al. 2020).

1.2 The complexity of community ecology

The role of individual species in shaping communities is well established, with numerous ideas put forward to explain the structure of ecological communities. Notable ecological processes such as biological trade-offs for habitat selection and species-specific responses, including interactions offer rationales for the observed coexistence of multiple species within habitats. However, decades of research have demonstrated that there is yet to be a uniformly

1

accepted theory explaining the structure of ecological communities (Lawton 1999; Loreau 2010; Eldijk et al. 2020).

The two opposing views centre on whether ecological communities are self-organised and independent systems or simply an assemblage of species with no clear geographical boundaries (Lawton 1999). These two views were characterised as the organismic concept of communities and the individualistic concept. Clement believed that communities were essential components of ecosystem functioning with their own structure and functioning, while Gleason explained that a community is an assemblage of species that coexist mainly due to similarities in their physiological requirements and resilience (Gleason 1926; Clement 1936). In opposition to Clement's view, Gleason argued that communities result from species-specific responses to the environment rather than from interactions between species (Gleason 1926; Loreau 2010). He noted that while some assemblages of species were relatively uniform and stable within certain areas, distinctly structured communities do not commonly occur in nature (Gleason 1926). Instead, species occur independently along an environmental gradient, suggesting that communities are far more complex, and associations between species are more dynamic than Clement initially indicated (Loreau 2010; Eldijk et al. 2020). However, our current understanding of how communities are structured is far more complex, with less emphasis on the classification of species assemblages into discrete communities but rather on understanding the processes that allow species to coexist within communities (Götzenberger et al. 2012).

The early work of Grinnell (1917) and Elton (1966) on the development of the niche concept furthered our understanding of species distribution patterns and community structure. Grinnell (1917) first used the term niche in reference to the environmental factors needed by a species for its distribution. Elton (1966) later defined the term niche as the role of a species

2

in an ecosystem along with its interactions with other species. This led to numerous debates in the field of ecology as the niche concept suffered from ambiguity and incorrect use (Soberón and Peterson 2005). As it would later be called, niche theory was formalised by Hutchinson (1957) with his work on differentiating between the fundamental and realised niche (Blonder 2018).

The emergence of neutral theory proposed an alternative to the current niche theory by emphasising the unstable nature of ecological communities and the role of stochasticity as the primary factor responsible for structuring ecological communities (Hubbell et al. 2001). Neutral theory proposes that all individuals across species are ecologically identical, and differences in an organism's niche are not needed to explain biodiversity patterns (Hubbel 2001). In modern times, neutral theory has found its place in community ecology as a null model for evaluating the roles of non-neutral processes such as adaptation and natural selection in shaping ecological communities. As community ecology continues to develop and change, there has been a shift from describing community patterns to understanding the processes underlying these patterns (Hubbel 2001; Chave 2004)

1.3 The structure of ecological communities

Ecological communities are complex biological systems characterised by trophic and non-trophic species interactions along with the physical structure of the environment (Elton 1946; Daniel Simberloff and Dayan 1991; McGill et al. 2006). In its basic form, an ecological community refers to a group of interacting species that co-occur within a given area (Lima 2002). A primary focus of modern-day ecological studies is to describe how species are distributed throughout their habitat by correlating species occurrence data with environmental variables (Paine et al. 2018). These types of studies are beneficial as they aid in monitoring the functionality and stability of an ecosystem (Cardinale et al. 2006) and aid in the

3

conservation of the biodiversity within (Schwartz et al. 2000). However, communities are dynamic in nature, with the composition and occurrence of species varying both spatially and temporally (Zuluaga 2015; Paine et al. 2018). Therefore, it is essential to consider species interactions in ecological studies as they form the basis of many community properties and processes (Costa-Pereira et al. 2018).

The structure of a community refers to the composition of the species within the community, the number of species present and their relative numbers (McGill et al. 2006). Habitat, ecosystem stability, and species interactions are all significant factors that influence community structure (Lepš 2004; Lawson and Moyer 2008). However, determining the exact role and importance that species interactions play in shaping ecological communities is no easy feat and often requires long-term ecological studies and a broad understanding of the ecology of all species concerned (Anderone and Luiselli 2000; Chalcraft and Resetarits 2003; Orrock et al. 2010). It is particularly important when the composition of ecological communities varies significantly within a region. A large body of research already addresses topics such as community richness (Harrison and Cornell 2008), the phylogenetic structure of communities (Cavender-Bares et al. 2009) and the relative abundance of species (Hubbell et al. 2001). However, one of the major challenges in understanding the effects of species interactions is that a species can co-occur with a different set of species at various locations within its geographic range (Bruckerhoff et al. 2021). When this is the case, the occurrence and intensity of interactions are likely to change between ecosystems (Chalcraft and Resetarits 2003). As all species are limited by either resource availability or the presence of predators, coexistence can be maintained when either species segregate and occupy slightly different ecological niches or display increased levels of interaction (Amarasekare 2003).

4

The habitat heterogeneity hypothesis (HHH) explains variation in community structure at a local scale (MacArthur and MacArthur, 1961; Cramer and Willig 2005). It states that structurally complex habitats allow more species to coexist by increasing the number of potential niches and means to exploit available resources (Amarasekare 2003). This hypothesis is often used to explain species diversity patterns locally, where heterogeneous ecosystems should support more species than homogeneous ones (Amarasekare 2003). The HHH suggests that increased habitat complexity leads to increased species diversity by facilitating specialization and competition through spatial segregation (Cramer and Willig 2005). This hypothesis has been applied to numerous ecological studies (Finch 1989; Willig et al. 2003), with the consensus being that maintaining heterogeneity benefits species richness, including in habitats threatened by human activity (Cramer and Willig 2005). Numerous studies of communities have assessed the ecological factors (including habitat heterogeneity) that affect species richness within habitats or across regions (Capizzi et al. 1995; Vitt et al. 2003; Mannocci et al. 2013; Steen et al. 2014a). However, many aspects of this subject, notably the impact of the co-occurrence of reptile species in a heterogeneous habitat, are still unclear and need further investigation (Steen et al. 2014a; Mohseni and Rad 2021).

1.4 Conservation challenges of reptiles

Reptiles represent one of the most diverse terrestrial vertebrates and constitute a significant component of global biodiversity (Pincheira-Donoso et al. 2013). They have one of the more successful evolutionary radiations with a diverse and highly adapted set of aquatic, terrestrial and arboreal taxa occupying nearly every continent on the planet (Pincheira-Donoso et al. 2013, Steen et al. 2014a; Portillo et al. 2019). Reptiles have long been poorly represented on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, with an even lower representation of detailed analysis of species' extinction risks (Böhm et al.

5

2013; Cox et al. 2022). Due to the current state of the world and global threats of deforestation, draining of wetlands and run-off pollution, there is an ever-growing need to understand the impact of our actions on biodiversity (Ortega et al. 2020).

South Africa is home to a diverse assemblage of reptiles with more than 400 species and over 50% of them are endemic to the region (Tolley et al. 2019). While these numbers are impressive, they are likely an underestimation as the reptile biodiversity in Africa remains poorly known compared to the temperate regions (Tolley et al. 2016). Reptiles play an essential role in ecosystems as both predator and prey species (Böhm et al. 2013). However, unlike birds and mammals, most reptile species have narrow distributional ranges and dispersal capabilities, making them more susceptible to threats (Böhm et al. 2013). Due to their sensitivity to anthropogenic threats, reptiles are facing ongoing mass extinction, with numerous species in decline (Gibbons et al. 2000; Böhm et al. 2013). Habitat loss is regarded as the primary factor responsible for reptile species loss, particularly in South Africa where large areas of land are cleared for agricultural purposes (Tolley et al. 2019). Unfortunately, it is difficult to fully assess the impact of habitat degradation on Africa's reptile biodiversity as less than half of all species have been assessed for extinction risk by the IUCN (Tolley et al. 2019).

Snakes represent over 30% of total reptile diversity (Uetz et al. 2020). They have an almost global distribution, being absent only from the Polar Regions (Araujo et al. 2006) and several islands. Snakes have adaptations that allow them to occupy most habitats, including aquatic, terrestrial, subterranean, or arboreal lifestyles, with some species able to utilise a variety of these habitats throughout their lives (Luiselli 2006b). All snakes are limbless, and many species are cryptic and possess smaller home ranges than other faunal species in a given ecosystem (Durso et al. 2011; Triska et al. 2017). Snakes are exclusively carnivorous, feeding

6

on various prey items, including invertebrates, fish, amphibians, avian, mammalian and reptilian taxa, with some species specialising in a single prey type (Keogh et al. 2000; França and Araújo 2007; Bellini et al. 2015). In recent years, snakes have emerged as an ideal group of study species to study patterns of species co-occurrences (McCauley et al. 2006; Pittman and Dorcas 2006; Steen et al. 2014a). The high level of specialization and microhabitat use exhibited by snake species, observed at even small spatial scales within ecosystems, make them a model study organism (Maritz and Alexander 2012; Edgehouse et al. 2014; Wiens 2018).

Snakes account for 30% of reptile species in southern Africa (Bates et al. 2014). While snakes have very few species of conservation concern (Bates et al. 2014) they are nevertheless integral members of the ecosystem, and their extinction could cause adverse ecological damage (Doherty et al. 2020). Current literature that assesses the status of snake species and their population trends is vastly limited compared to mammals and amphibians (Roll et al 2017). This makes it difficult to gauge the full impact of habitat loss on them, as baseline population data is absent mainly for snake communities (Reading et al. 2010).

Recent studies into the global conservation of reptiles have renewed interest in ecological studies of snakes due to their unique role in the trophic hierarchy. Importantly, these studies have identified gaps in our understanding of reptile ecology, including snake ecology that needs to be filled (Tolley et al. 2016). Past studies of snake assemblages in southern Africa often only describe the species richness or list of snake species within the area (Jacobsen and Randall 2013). Recent studies have begun to explore snake communities in a more detailed manner, along with the effects of anthropogenic habitat modification (Maritz and Alexander 2007), microhabitat use (Coombs 2016), indirect effects (McCauley et al. 2006), and conservation actions (Masterson et al. 2008) on those communities. However, many of these

7

studies do not explicitly consider fine-scale variations of snake communities in the presence of multiple interacting species and how they relate to the environment.

1.5 Snake communities

In snake communities, co-occurrence with other species and vegetation types is predicted to influence snake distribution and abundance (França and Araújo 2007; Masterson et al. 2008; Steen et al. 2014a). The restriction of cover, for instance, can restrict the abundance of snake species and their distribution by limiting the ability of those snakes to escape predation (Cox et al. 2009). Studies have found that the best predictors of snake community structure are often the species richness and abundance of snake prey communities (Arnold 1972; Capizzi et al. 1995; Anderone and Luiselli 2000), vegetation type (Reinert 1984), the presence of predators (Steen et al. 2014a) and indirect effects (McCauley et al. 2006). Snake coexistence (and therefore competition) may equally, if not more so than environmental factors, explain snake community structure as their ecology often places them as both predators and prey within the same food web (Steen et al. 2014a). Moreover, evidence suggests that many snake communities are structured by resource availability (Capizzi et al. 1995; Luiselli and Filippi 2006; Cox et al. 2009). If this is the case, sympatry may be facilitated by the diversity and abundance of prey available within a habitat (Capizzi et al. 1995; Steen et al. 2014a).

1.5.1 Biotic interactions and coexistence in snake communities

Competitive interactions have been shown to influence snake community composition and community structure (Capizzi et al. 1995; Luiselli 2006b; Steen et al 201a; Bellini et al. 2015). The evidence for the role of competition in shaping snake communities includes food resource partitioning (Capizzi et al. 1995; Bellini et al. 2015; Tokota 2021), dietary shift in the presence of a potential competitor (Luiselli 2003; Perkins et al. 2020), and competitive

8

exclusion in the presence of a predator (Steen et al. 2014a). The degree and severity to which competitive interactions influence snake community composition

As competition plays a significant role in determining the structure of snake communities, it is vital to understand the factors that allow multiple snake species to coexist in a given habitat. The best-documented explanation for this is the way snakes partition resources. Habitat is the primary resource partitioned in most vertebrate communities (Capizzi et al. 1995). However, this is not always true in snake communities. Cox et al. (2009) noted that while competition could exclude competitively inferior snake species, they observed multiple snake species utilising cover objects. They concluded that food partitioning shapes the community structure of sympatric snake populations (Edgehouse et al. 2014). One possibility for the relatively high species richness seen in some snake communities is that while they might prey on the same prey type, they partition the food by feeding on different prey sizes (Luiselli 2006a).
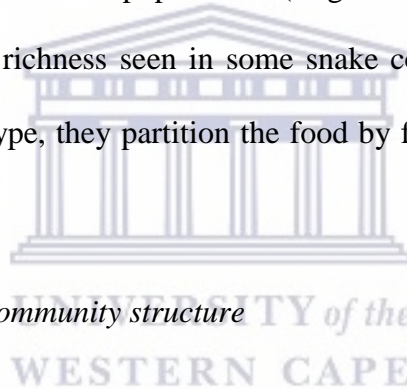
1.5.2 Abiotic drivers of snake community structure

Environmental variables affect ecosystems both spatially and temporally, and these effects can vary even in similarly structured ecosystems (Bellini et al. 2015). Numerous explanations have been put forward to aid in our understanding of the effects of abiotic factors on species richness and abundance of snake species (Reinert 1984; Luiselli and Filippi 2006). Abiotic factors are known to trigger behavioural responses in snakes affecting mating behaviour, reproduction, and hibernation. While it is clear that snake species make use of their available habitats in a non-random way (Reinert, 1984), we still do not fully understand the effects of abiotic factors on the diversity and abundance of snake communities (Luiselli and Filippi 2006).

9

The ecology and physiology of snake species are strongly linked to the thermal environment (Piatti et al. 2019). It dramatically affects how snakes interact with and select suitable habitats to meet their ecological requirements (Eskew and Todd 2017). Environmental changes may initially affect their physiological processes over time affecting their individual fitness. Many of their physiological processes are temperature dependent and nearly all aspects of their ecology and physiology will be affected either directly or indirectly by variations in environmental conditions (Kiyoshi 2016). Furthermore, different environmental stressors will result in different responses in their physiology and fitness-related characteristics (Sasaki et al. 2016). Therefore, studies aimed at assessing snake communities need to consider the direct and indirect responses of abiotic factors on snakes as these factors are likely to influence their community structure (Lima 2002).

UNIVERSITY of the
WESTERN CAPE

1.6 Problem statement, aim and objectives

Despite the potential importance of habitat heterogeneity, species co-occurrence, and shared predators and prey, studies linking these attributes to explain snake community structure are rare and remain unexplored in southern Africa. This paucity of studies limits our understanding of how snake communities function and possibly how to manage them. Therefore, I aimed to investigate the response of a local snake community to the effects of the presence and abundance of snake competitors, potential predators, prey, and vegetation structure in a fynbos ecosystem. More specifically, my objectives included:

1.   Characterise the snake communities at ten sites in Koeberg Private Nature Reserve.

2.   Quantify the diversity and abundance of prey species at each site by developing an index of prey abundance that accounts for the interspecific variation in how different snake species use different prey types.

3.   Quantify predator abundance and diversity at each site.

4.   Test the hypotheses that individual snake species abundances can be explained by combinations of the abundance of other snakes, prey availability, predator abundance, and vegetation structure.

5.   Test the hypothesis that inter-site differences in snake communities can be explained by the abundance of other snakes, prey availability, predator abundance, and vegetation structure.

11

Chapter 2: Methods

2.1 The focal ecosystem

The Cape Floristic Region (CFR) is considered one of the richest global biodiversity hotspots in plant diversity and endemism (Rebelo et al. 2006; Krupek et al. 2016). *Fynbos* is regarded as the most iconic of these vegetation types, occurring predominantly in winter rainfall areas along the coast and mountainous areas associated with a Mediterranean climate (Rebelo et al. 2006). The fynbos environment is characterized by nutrient-poor soils and regular fire regimes coupled with cold, wet winters, and hot and dry summers, resulting in a diverse assemblage of floral and faunal species (Mukundamago 2016).

Cape Flats Dune Strandveld (CFDS) is a vegetation type endemic to coastal regions of the Western Cape province of South Africa and is considered one of the smallest and most vulnerable vegetation types in the fynbos biome (Mukundamago 2016). Historically, strandveld was one of the dominant vegetation types throughout the Western Cape; however, habitat destruction caused by cultivation and urban encroachment, along with the invasion of alien plant species (e.g., *Acacia cyclops*, *Acacia saligna*, *Pinus radiata,* and *Eucalyptus salmonphloia*) have greatly reduced strandveld vegetation (Mukundamago 2016). Introduced *Acacia* species form the bulk of invasive alien species in the CFDS. They were introduced to South Africa around 1845 for dune stabilization but have since invaded large coastal and lowland areas (Krupek et al. 2016; Mukundamago 2016). Alien plants and cultivation are known to alter fire regimes and affect nutrient cycling resulting in large-scale changes in indigenous ecosystems (Baker 1992). Conservation and restoration of these degraded vegetation types are thus essential.

Large-scale restoration of fynbos in the Western Cape has been a priority for several years (Mukundamago 2016). Cape Flats Dune Strandveld is managed through prescribed burning,

12

thus allowing this vegetation type to persist. However, re-establishment areas of CFDS are relatively small and continuously under threat making conservation efforts difficult. Koeberg Private Nature Reserve (KPNR) is one such area where CFDS is managed, forming an essential part of the City of Cape Town's biodiversity network (Krupek et al. 2016). The KPNR conserves a unique combination of faunal and floral species, with CFDS as the primary vegetation type. Among the native faunal species that occur within the reserve boundaries, the reserve supports a snake community that consists of numerous iconic and well-known snake species, including but not limited to cape cobras (*Naja nivea*), boomslang (*Dispholidus typus*), mole snakes (*Pseudaspis cana),* and skaapstekers (*Psammophylax rhombeatus*).

2.2 Koeberg Private Nature Reserve

Koeberg Private Nature Reserve (18° 26' E, 33° 41' S) is a protected area along the west coast of South Africa (Figure 1: Koeberg Private Nature Reserve (KPNR) with reserve boundaries and sampling sites along the west coast of the Western Cape Province of South Africa. The nature reserve covers an area of approximately 3 000 ha and is located approximately 30 km north of Cape Town, Western Cape, South Africa. The temperate, Mediterranean climate of the region is characterized by winter rainfall and an average annual rainfall of 372 mm (Cape Weatherwise International 2020). Air temperatures are strongly affected by the Atlantic Ocean, with average daily maximum temperature ranging from 17 °C in winter to 28 °C in summer (Harrison and Cornell 2008). The reserve is home to two major veld types: West Coast Strandveld and Cape Flats Dune Strandveld (Eskom Holdings SOC Limited 2014). The vegetation is characterised by small-leafed, evergreen shrubs, succulents, and groundcover plants and can support a diverse assemblage of vertebrate and invertebrate faunal species despite being considered nutrient-poor (Eskom Holdings SOC Limited 2014). Strandveld experiences infrequent burns; however, fires have occurred far more frequently since the

13

introduction of *Acacia* spp. (Mukundamago 2016). Several conservation projects in the reserve are aimed at eradicating alien *Acacia saligna* (Port Jackson) and *Acacia cyclops* (Rooikrans) (Eskom Holdings SOC Limited 2014).

2.3 Site selection

The Maritz lab at the University of the Western Cape carried out a snake community pilot study at KPNR between 2016 and 2017 (B. Maritz, unpublished data). During this period, 250 artificial cover objects (ACO) were installed at 10 sites across KPNR. Artificial cover objects were deployed in a 5 x 5-grid pattern over approximately 100 m^2 at each site. ACOs were made of 21 mm thick shutter ply wooden boards measuring 600 mm x 600 mm, and were checked intermittently throughout the two years. During the pilot study, 306 unique herpetofaunal observations were recorded, including 112 snake records. The pilot study provided important information on snake species' likely occupancy and habitat preferences within the reserve. Eight of the original sites installed during the pilot study were used in my work, and an additional two sites were established, producing ten sampling sites. Sites were stratified across the reserve to include a mosaic of vegetation types. Sites were classified into one of three vegetation type categories based on their level of disturbance. These included burnt strandveld, cleared strandveld, and undisturbed strandveld. Sites situated in the reserve area affected by a fire in 2016 were classified as burnt sites (n = 3). Sites that had been cleared of invasive alien *Acacia* spp. were considered cleared sites (n = 3), and lastly, sites with no noticeable signs of disturbance were classified as undisturbed (n = 4).
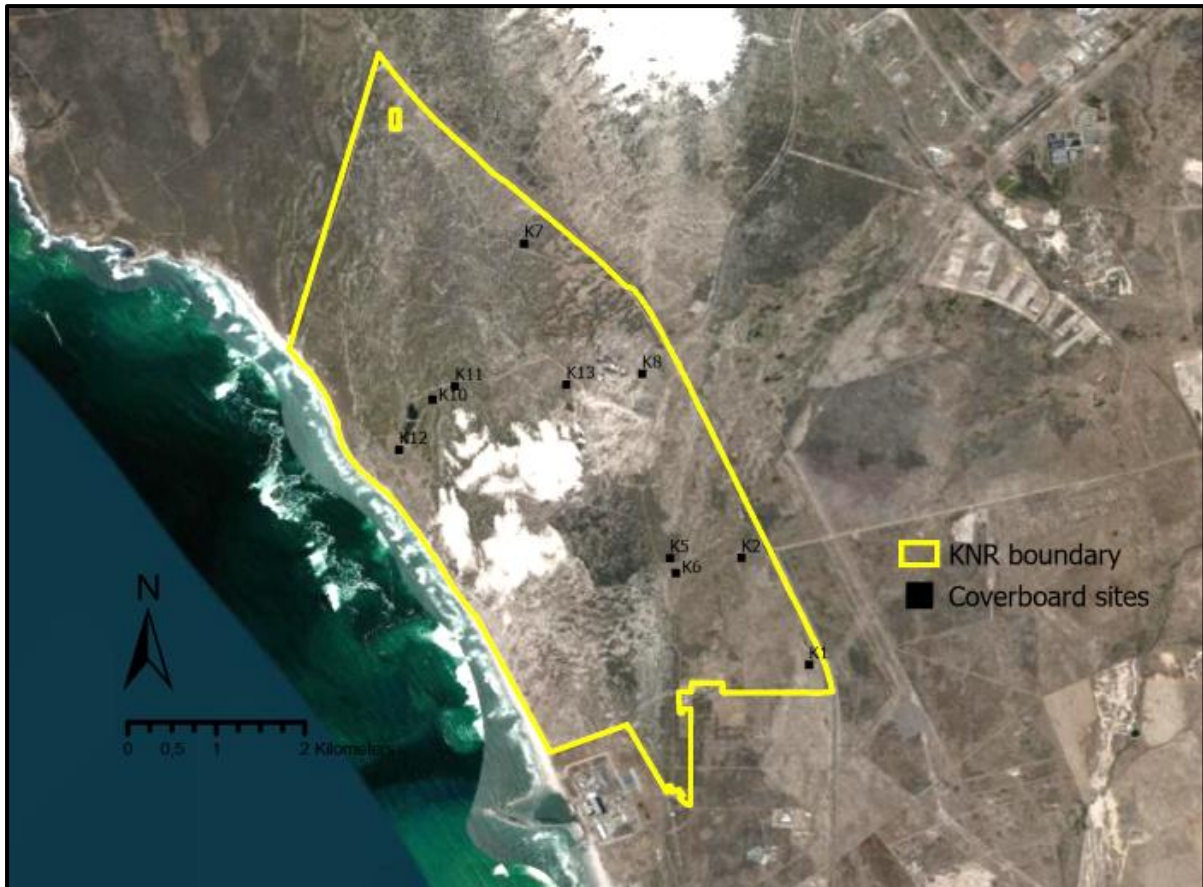
14

Figure 1: Koeberg Private Nature Reserve (KPNR) with reserve boundaries and sampling sites along the west coast of the Western Cape Province of South Africa. Artificial Cover Object sites are designated with an alphanumeric identifier. Sites K3 (burned in the 2016 fire) and K4 and K9 (removed due to access issues) are not reflected in the image. Image: Google Earth.

2.4 Sampling the snake community

2.4.1 Artificial cover object surveys

For my study, snake surveys were conducted from February 2018 to April 2019. This consisted of checking all 250 ACOs in the morning, once every two weeks. This produced a total sample effort of 24 sampling days. Throughout the study, I also recorded incidental records while checking ACOs, using the nearest ACO as a reference point for incidental

15

detections. Snakes were identified to the species level before being captured. I took measurements for body length (snout-vent length [SVL] and tail length) using a ruler (measured to the nearest 1 mm) and body mass using a digital field balance (to the nearest 0.1 g) from each snake. Snakes were marked by scale clippings of their ventral scales (Plummer and Ferner 2012) before being released at the point of capture. Recaptured snakes were re-measured before being released but were not re-marked.

2.4.2 Characterising site-specific snake communities

The first objective of my study was to characterise site-specific snake communities. To assess sampling completeness, I plotted a rarefaction curve for each site. Rarefaction curves are commonly used in ecological studies to assess species richness based on sampling effort and the abundance of sampled individuals (Cayuela et al. 2015). They plot the cumulative number of species represented by an increasing number of individuals. Rarefaction curves allow comparing multiple sites varying in sample size via standardisation of the data to the same number of individuals (Gotelli and Colwell 2009). I used the R package *vegan* (Oksanen 2017) to assess sampling completeness and estimate total richness for each site (Chiu et al. 2014).

Next, I quantified five community variables (species richness, Chao1 species richness, evenness, abundance, and biomass) for each site in R using the package *vegan*. The community variables describe different aspects of community structure and are used in ecological studies to inform community composition (Buchheister 2014). I quantified species richness by counting the number of species of snakes detected at each site. I calculated the Chao 1 estimator to estimate the expected species richness at a site based on the number of rare species represented by one or two individuals (Chao 1984). I calculated evenness at each site using Pielou's measure of evenness (Alatalo 1981). Abundance for each snake species

was measured as the total number of unique snakes caught and marked during ACO surveys, with overall abundance for the site being the sum of the abundance for each species. The total biomass of each snake community was defined as the summed mass of all unique snakes that were caught during sampling. While I did recapture a few individuals, the mass that I used in my analysis was the initial mass of each snake.

2.5 Characterising snake diets

A literature review was performed to identify which prey species are known to occur in the diet of each snake species detected during sampling. The literature review assessed published literature sources as summarised in Maritz and Maritz (2020). For each snake species, I recorded general descriptions of diet and used these to infer whether mammals, birds or their eggs, amphibians, lizards, or snakes are known prey items for the snakes in the community. I was then able to construct an incidence-based dietary matrix, which indicated the presence of a prey item in the diet of each snake species (Appendix 2).

2.6 Sampling the snake prey community

2.6.1 ACO sampling for snake prey

Prey items (including small non-snake squamates, amphibians, and small mammals) found under ACOs were identified to species level, weighed, and measured before release. I calculated the species richness for prey items, including snakes, as the number of species detected under ACOs at each site.

2.6.2 Visual surveys for avian snake prey

I surveyed bird species richness and abundance for two days in August 2018, October 2018, February 2019, and May 2019. Four observers sampled each site for 40 min recording the total number of species detected and the total number of individuals of each species detected,

making an effort not to recount individual birds. I estimated a proxy of the abundance of all avian prey at each site as the number of individual birds detected per survey, averaged across the eight surveys per site.

2.6.3 Sherman trapping for mammalian snake prey

Sherman trapping was used to measure the species richness and abundance of small mammals at each site. I sampled each site for seven consecutive nights in August 2018, October 2018, February 2019, and May 2019 totalling 3360 trap nights (A trap night is one trap set for one night). At each site, twelve PVC Sherman traps were placed in a 4 X 3-grid pattern in the centre of each site. Traps were baited in the early evening before sunset (16:00) and inspected the following morning (08:00). Traps were baited with a mixture of peanut butter and oats. Additionally, a piece of cotton wool was placed in each trap as nesting material during colder months. Animals were marked with a non-invasive, temporary fur clipping by cutting a small section of fur on the right rump before being released at the point of capture. Small mammal communities were characterised by calculating the species richness and abundance at each site. I used the total number of species trapped at each site for species richness. I calculated a proxy of the abundance of each species as the sum of individual (non-marked) animals across all four surveys.

2.6.4 Trap array sampling for snake prey

Trap arrays were used to measure the species richness and abundance of species unlikely to use ACOs or Sherman traps. I collected trap data for seven consecutive nights at each site in August 2018, October 2018, February 2019, and May 2019 totalling 1120 pit trap nights. At each site, a four-armed drift array and pitfall traps were deployed at the centre of the site. Drift fences were constructed using wooden stakes stapled to green shade cloth, and four 20l buckets (pitfall traps) were placed at each end of the fences with a central bucket placed at

18

the centre. A damp cloth was placed in each pitfall to provide moisture and cover for animals caught in pitfall traps. Funnel traps were initially added to each trap array but proved ineffective at capturing the target species, snakes, and for that reason, their results were omitted from this study. Prey species were characterised by calculating the species richness and abundance at each site. I used the total number of species trapped at each site for species richness. I calculated a proxy of the abundance of each species as the sum of individual (non-marked) animals across all four surveys.

2.7 Calculating a proxy for site-specific snake prey abundance

Estimating a single proxy for prey abundance is challenging because of the relative importance of different prey types in the diets of different snakes in the community. I utilised the incidence-based dietary matrix (see Section 2.5) and grouped the prey species (lizards; snakes; amphibians; birds and their eggs; mammals; Table 2). A zero value was scored if the prey type was not known from the diet according to the literature.

To understand which prey types contribute most to the diets of snakes across the entire community, I calculated the Community-Wide Prevalence (CWP) of each prey type as the number of snake species that consumed a given prey type, divided by the total number of snake species in the community. Next, I calculated a Prey Importance score (PI) for each prey type as that prey type's CWP divided by the maximum CWP measured across all prey types. Therefore, in a simple hypothetical example that includes only two prey types, where prey type one is consumed by two-thirds of all snake species and prey type two is consumed by one-third of the community, CWP would be 0.67 and 0.33 for prey types one and two respectively, and PI would be 1.00 and 0.50 for prey types one and two respectively. This could then be interpreted as saying that prey type one is twice as important for the overall snake community as prey type two.

To incorporate the survey measures for the abundance of different prey types across the ten sites, I created a matrix of all sites by the five prey types and populated it with the prey abundance data from my surveys. Next, I calculated the relative abundance of each prey type across the ten sites by dividing the abundance of a given prey type at a given site by the sum of the abundance of that prey type across all sites. To incorporate the importance of a given prey type to the snake community, I multiplied these relative abundance measures by their corresponding PI scores to provide a proxy for the significance and relative abundance of prey types at each site. Finally, I summed the resultant values across each prey type yielding my final proxy for prey abundance at each site.

2.8 Sampling the snake predator community

A wide diversity of species includes snakes in their diets, including carnivorous invertebrates, reptiles, mammals, and birds (Martins 1996; Rowland et al. 2012). While many species that feed on snakes do so opportunistically, several predators are known to feed or specialise exclusively on snakes (Martins 1996). This specialized feeding behaviour, referred to as ophiophagy, is observed in numerous species in southern Africa. For this study, species were classified as snake predators if snakes were included in their diet. Snake predators were grouped by taxonomic affinity; reptiles, mammals, or birds.

2.8.1 Reptiles

Ophiophagy has been noted in several reptile genera, including lizards (Mayers et al. 2005, Karameta et al. 2015), turtles (Lovich et al. 2010), and snakes (Rowland et al. 2012; Layloo et al. 2017; Maritz et al. 2019a; Portillo et al. 2019). Many snake species include other snakes in their diets, mostly opportunistically but several exclusively (Rowland et al. 2012). In southern Africa, ophiophagy is known to occur in several snake genera, including the *Naja* (Shine et al. 2007; Layloo et al. 2017; Maritz et al. 2019a), *Thelotornis* (Shine et al. 1996;

20

Maritz et al. 2019b), *Psammophis* (Kusamba et al. 2013; Shine et al. 2017), *Homoroselaps* (Portillo et al. 2019) and several others. I categorised snake species detected at a site as snake predators if the literature reflected at least one record of ophiophagy in their diet.

2.8.2 Birds

The importance of snakes in bird diets has been noted in numerous studies (Martins 1996; Martín and López 1996; Maritz and Scott 2010). Birds are ecologically diverse and occur in many habitats (Whelan et al. 2015). Their relative abundance and ecological importance make them important predators of snakes and most reptile species (Martins 1996; Maritz and Scott 2010). Not all bird species prey on snakes. Raptors are predatory birds that actively hunt and prey on small vertebrates, including snakes. Raptors are mainly diurnal, visually-oriented predators that actively search and hunt their prey (Martins 1996). Therefore, snakes basking in the open are easy prey for these birds (Selas 2001). I included all raptors and birds known to include snakes in their diet as snake predators (Hockey et al. 2005).

2.8.3 Mammals

Numerous mammal species are known to prey on snakes (Voss and Jansa 2012). Within southern Africa, ophiophagous mammals include the honey badger (*Mellivora capensis*; Begg et al. 2003), striped polecat (*Ictonyx striatus*; Lariviere 2002) and cape grey mongoose (*Galerella pulverulenta*; Cavallini and Nel 1990). Snakes are likely only minor prey items in the diets of canids, felids and talpid species (Voss and Jansa 2012). As far as the literature suggests, no mammals prey exclusively on snakes, with many species either being generalist carnivores or omnivores (Voss and Jansa 2012). Therefore, all carnivorous mammal species detected were identified as snake predators.

2.8.4 Camera trapping for snake predators

Five camera traps (Cuddeback Model C2) were placed at the ACO sites to detect the presence of potential snake predators. I used the protocol based on previous camera trapping surveys done within the reserve (Forgus 2018). Cameras were fixed to wooden stakes and placed along existing game trails, with the cameras positioned approximately 30 cm off the ground. The cameras were left in the field for two weeks before being relocated to new ACO sites. This process was repeated for one year (June 2018 – June 2019), resulting in 189 camera trap nights for each site, totalling 1890 camera trap nights observing ACO sites.

All camera trap images were examined, and all photographed animals were identified to species level. To determine the effectiveness of the camera trapping, I plotted a sampled-based rarefaction curve (Gotelli and Colwell 2001). The curve indicates the rate at which new species were detected to the number of surveys conducted. The species richness for snake predators was recorded as the total number of species detected known to include snakes in their diet. Additionally, species abundance was recorded as the total number of photos taken of a species throughout the sampling period.

2.8.5 Visual surveys for avian snake predators

Visual surveys for snake predators were carried out simultaneously with snake prey visual surveys (see 2.6.2 above). I used available literature to compare the diets of all detected bird species at my study site to determine which species prey on snakes (Hockey et al. 2005).

2.9 Calculating a proxy for site-specific snake predator abundance

To assess the relationship between predators of snakes and snake communities, I quantified the species richness and abundance of predator species at each site. Species richness was the total number of species detected during the sampling period known to consume snakes. For

22

abundance, I used the number of individuals for each species observed. To do this, I pooled the data from both predator-sampling methods.

2.10 Statistical analysis

Snake count data from each sampling method were pooled into a site-by-species matrix for further statistical analysis. The multivariate abundance data formed the response variable for the generalised linear models (GLM), testing for differences in individual species responses and community responses with predictor variables (vegetation type, predator and prey abundance and species richness), and interactions. Vegetation type was the only categorical variable used in my analysis and "undisturbed" was used as the reference level. All statistical analyses were performed using the R statistical computing program version 3.6.4 (R Core Team 2020).

Snake community structure was assessed using the R package *mvabund* with the function *manyglm* and *anova.manyglm*, using a Poisson distribution accounting for the overdispersal of the data. This type of analysis differs from distance-based multivariate analysis as it accounts for the mean-variance relationships, commonly seen in abundance data containing many zeros. It works by fitting multiple GLMs to each variable simultaneously and using the *anova.manyglm* function for hypothesis testing. Resampling-based hypothesis testing can then be used to make community and species-specific inferences about which predictors significantly affect snake community structure. All variables were explored for collinearity before including them in the models. Univariate test statistics and p-values were calculated for each species in the model to indicate their relative contribution to the overall variance among snake communities. This was done to characterise the snake communities at each site and assess each species' relative contribution to the community composition.

23

I tested the hypothesis that inter-site differences in snake communities can be explained by the abundance of other snakes, prey availability, predator abundance, and vegetation structure using my four snake community metrics. I assessed each of my snake community metrics (species richness, estimated species richness, abundance, biomass) by creating a set of GLM models with each snake community metric as the dependent variable, and vegetation, predator abundance, predator species richness, prey abundance, prey species richness, and their interactions as the explanatory variables. Generalised linear models with a Poisson distribution were used to analyse the response of the community metrics to the relevant response variables. Additionally, to assess the performance of each model, an intercept-only model "null model", was constructed and included in the analysis.

GLMs were constructed for each of the ten snake species to investigate individual snake species' responses to explanatory variables. This was done by creating a set of models for each species with their potential prey, predators, and vegetation type. Where relevant, the optimal model was determined by comparing models based on the Akaike information criterion (AICc) using the dredge function in the MuMin package.

Chapter 3: Results

3.1 Snake communities

3.1.1 Snake survey results

A total of 156 individual snake records from ten species were recorded across 24 ACO surveys between 2018 and 2019 (Table 1). Of these records, 52 were recaptures, and seven were incidental sightings while sampling sites. The psammophid snakes *Psammophylax rhombeatus* and *Psammophis crucifer* were the most abundant snake species across all sites, accounting for 52 % and 26 % of all snake capture records. The remaining nine detected species were represented by fewer samples with the total number of detections per species ranging from two to five across all sites. *Rhinotyphlops lalandei* was the only snake species detected using trap array sampling, while *Naja nivea* was only recorded incidentally while working at sites. I recorded the highest number of species from site K10 where only *Crotaphopeltis hotamboeia, Pseudaspis cana* and *Psammophis leightoni* were not detected during the study period.

Table 1: Total number of individuals (and recaptures) for each snake species detected at Koeberg Private Nature Reserve. Sites are allocated alphanumeric identifiers. Sites K3, K4, and K9 are not shown.

	K1	K2	K5	K6	K7	K8	K10	K11	K12	K13	All sites
Colubridae											
Crotaphopeltis hotamboeia									2		2
Dasypeltis scabra			1				1 (3)	2 (1)			4
Elapidae											
Naja nivea				1	1		1				3
Atractaspididae											3
Homoroselaps lacteus	1 (3)						1				2
Lamprophiidae											
Lycodonomorphus inornatus							3 (2)				3
Psammophiidae											
Psammophis crucifer	3 (2)	5	5 (1)	1	6 (5)	5 (1)	2	1	1	2	31
Psammophis leightoni				1	2			1	1		5
Psammophylax rhombeatus	5 (2)	6 (1)	6 (6)	4	7 (5)	8 (4)	3(4)	4 (3)	3	1	47
Pseudaspididae											
Pseudaspis cana	1		1	1							3
Typhlopidae											
Rhinotyphlops lalandei							4				4
All species	**10**	**11**	**13**	**8**	**16**	**13**	**14**	**8**	**7**	**3**	**106**

3.1.2 Snake sampling completeness

Visual inspection and extrapolation of the individual-based rarefaction curves suggest that the snake community at each site was not well sampled (Figure 2). The curves that have not plateaued (notably at K6 and K12) suggest that further sampling would yield additional snake species at these sites. This finding necessitated the use of species richness estimators described below.
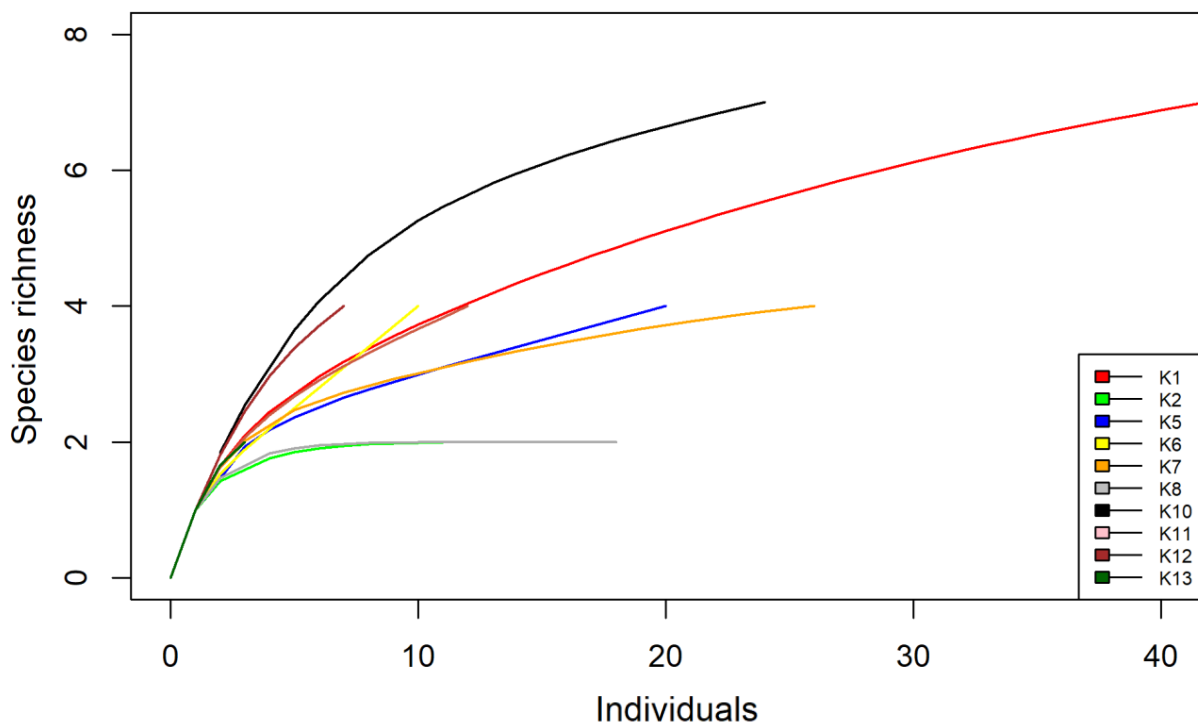
Figure 2: Individual-based rarefaction curve for snake communities for each site based on species count data for ACO sampling surveys from 2018 – 2019 within Koeberg Private Nature Reserve

3.1.3 Metrics of snake community variation

I measured five diversity metrics from the snake sampling data to assess snake communities across sites: species richness, abundance, total biomass, Chao1 estimator, and Pielou's evenness (Table 2). Because of the variability in how the rarefaction curves levelled out (or failed to level out), estimated richness (e.g., Chao1) is likely to reflect the snake community diversity better than observed species richness

Table 2: Summary statistics for snake communities at ten sites across KPNR

	K1	K2	K5	K6	K7	K8	K10	K11	K12	K13
Species richness (S)	4	2	4	5	4	2	7	4	4	2
Abundance	10	11	13	8	16	13	15	8	7	3
Total Biomass (g)	229	411	215	106	229	262	230	140	60	70
Chao1	5	2	5	11	4	2	9	5	5	2
Pielou's evenness (J)	0.84	0.99	0.81	0.86	0.84	0.96	0.93	0.88	0.92	0.92

3.2 Snake diet literature survey results

The literature review of the diets of the snakes detected during my study revealed the following information.

3.2.1 Crotaphopeltis hotamboeia (Herald snake) Laurenti, 1768

Crotaphopeltis hotamboeia is one of six small to medium-sized colubrid snakes within the genus *Crotaphopeltis*, endemic to the African continent (Keogh et al. 2000). They occur throughout southern Africa's eastern and southern parts and are associated with mesic habitats (Bates et al. 2014). A mildly venomous and nocturnal snake, the diet of *C. hotamboeia* consists predominantly of amphibians but also includes squamate reptiles (lizards) and small mammals (Keogh et al. 2000; Maritz and Maritz 2020).

28

3.2.2 Lycodonomorphus inornatus (Olive house snake) Dumeril, Bibron and Dumeril, 1854

Lycodonomorphus inornatus is a colubrid snake endemic to South Africa and Swaziland, occupying moist coastal bushveld, fynbos and grassland habitats (Bates et al. 2014). A non-venomous constrictor, the diet of *L. inornatus* consists of amphibians, reptiles, small mammals, and other snakes (Branch 1998; Maritz and Maritz 2020). Birds have been noted in the diet of *L. inornatus* with predation records of *Promerops cafer*, along with two records from captive *L. inornatus* feeding on an unknown Passeriformes and *Poephila acuticauda* (Maritz and Maritz 2020).

3.2.3 Dasypeltis scabra (Rhombic egg-eater) Linnaeus, 1758

Dasypeltis scabra occurs throughout most of the African continent. They are nocturnal foragers able to climb shrubs, trees and rock faces in search of food but will also prey on ground-nesting bird eggs (Bates and Little 2013). *Dasypeltis scabra* is a bird egg specialist capable of consuming the eggs of most bird species (Gartner and Greene 2008). A recent study by Barends and Maritz (2021) suggests that *D. scabra* are competing with much larger oophagous competitors, which could be a limiting factor for their diets in the wild. Bates and Little (2013) noted that *D. scabra* could prey on the eggs of birds as large as the African Sacred Ibis (*Threskiornis aethiopicus*), measuring 39.7 to 51.2 mm in diameter (Hockey et al. 2005). A report by Krupa (1985) noted a captive *D. scabra* successfully swallowing a domestic duck egg with a length of 65 mm and a maximum width of 46 mm.

3.2.4 Homoroselaps lacteus (Spotted harlequin snake) Linnaeus, 1758

Homoroselaps lacteus is a small semi-fossorial snake endemic to the southern African region. It occurs in sandy substrates and under rocks throughout its range (Bates et al. 2014). The diet of *H. lacteus* consists of elongated squamates, including legless skinks, blind snakes and lizards (Portillo et al. 2019; Maritz and Maritz 2020).

29

3.2.5 Psammophylax rhombeatus (Spotted grass snake) Linnaeus, 1758

Psammophylax rhombeatus, or spotted skaapsteker, is a widespread and abundant psammophid snake endemic to southern Africa (Bates et al. 2014). They inhabit a range of habitats, including grasslands, fynbos, savanna and semi-desert areas (Bates et al. 2014). *Psammophylax rhombeatus* is a fast-moving diurnal snake that actively hunts its prey (Cottone and Bauer 2008). It exploits a diverse array of prey taxa, including invertebrates, amphibians, reptiles, birds, and mammals (Cottone and Bauer 2010; Shine et al. 2017; Maritz Maritz 2020).

3.2.6 Psammophis crucifer (Cross-marked grass snake) Daudin, 1803

Psammophis crucifer occurs throughout South Africa and the eastern regions of Zimbabwe, in grasslands and fynbos habitats (Bates et al. 2014). It is a mildly venomous snake feeding predominantly on reptiles such as lizards but has been noted to feed on frogs (Cottone and Bauer 2010). Dietary analysis of *P. crucifer* by Cottone and Bauer (2010) noted that *P. crucifer* preyed on other snakes (*Duberria lutrix* and an unknown *Psammophis* sp.). Additionally, records from the Facebook predation records group note *P. crucifer* preying on (*Duberria lutrix*, *Psammophylax rhombeatus, Philothamnus natalensis,* and an unknown *Psammophis* sp.; Maritz and Maritz 2020).

3.2.7 Psammophis leightoni (Cape sand snake) Boulenger 1902

Psammophis leightoni is endemic to the western regions of the Western Cape, where it occurs in sand fynbos and strandveld habitats (Bates et al. 2014). Taft et al. (2021) assessed the genetic differentiation between *Psammophis namibensis*, *Psammophis trinasalis* and *Psammophis leightoni* and proposed that they represent a single species. This revision would increase the distribution of *Psammophis leightoni* further east into South Africa and extend it northwards into Namibia (Bates et al. 2014, Taft et al. 2021). This snake preys on reptiles such as lizards and small mammals and includes other snakes (Shine et al. 2017).

3.2.8 Pseudaspis cana (Mole snake) Linnaeus, 1758

Pseudaspis cana is widely distributed throughout southern Africa, occupying various habitats but is notably absent from forested areas (Bates et al. 2014). While not venomous, mole snakes are large-bodied constrictors easily able to overpower their prey (Evans et al. 2019). Their diet consists mainly of small mammals such as moles and rodents and includes birds, bird eggs and amphibians (Dyer 1996; Maritz and Maritz 2020). Dyer (1996) and Calf (2004) noted seabird egg predator records by mole snakes from Robben Island. Dyer (1996) also recorded a young mole snake consuming a clicking stream frog. These records suggest that mole snakes will opportunistically feed on various prey items when available.

3.2.9 Rhinotyphlops lalandei (Delalande's beaked blind snake) Schlegel, 1839

Rhinotyphlops lalandei is a widespread burrowing snake endemic to southern Africa. This fossorial species uses its hard beak to burrow through hard substrates (Bates et al. 2014). It spends most of its life underground, feeding on ants and their eggs (Webb et al. 2001). None of the prey taxa that we sampled includes prey species for *R. lalandei*; therefore, it was not included in the dietary analysis.

3.2.10 Naja nivea (Cape cobra) Linnaeus, 1758

Naja nivea are large-bodied elapid snakes that occur across the western region of southern Africa (Bates et al. 2014). Throughout their range, they occupy a variety of biomes (Bates et al. 2014; Layloo et al. 2017). *Naja nivea* are dietary generalists feeding on a wide variety of prey types, including amphibians, reptiles, birds and small mammals (Layloo et al. 2017). An examination of the diet of *N. nivea* by Layloo et al. (2017) suggested that snakes make up as much as one-third of their diet. Additionally, cannibalism has been noted within the species (Layloo et al. 2017; Maritz et al. 2019a; Maritz and Maritz 2020).

3.3 Prey communities

3.3.1 ACO prey sampling results

During the survey period, artificial cover object sampling resulted in 288 records from 16 prey species. Prey species included seven species of lizard along with a single small mammal species (Table 3). Snake species found during ACO surveys were also included as prey species because of the detection of multiple ophiophagous snake species.

Table 3: Number of non-snake prey items, per species, per site, captured during ACO sampling at KPNR. No prey items were captured at K13 during ACO sampling.

	K1	K2	K5	K6	K7	K8	K10	K11	K12	K13
Reptiles										
Pachydactylus austeni	1		1							
Pachydactylus geitje	1	1	8		3	8	6	6	8	
Acontias meleagris			2						1	
Scelotes bipes		1		1					1	
Trachylepis capensis	52	7	7	3				2	1	
Trachylepis homalocephala					1	1			3	
Trachylepis variegata					1		2	5	2	
Mammals										
Myosorex varius	11	1						1		

32

3.3.2 Visual prey sampling results

Visual prey sampling resulted in 291 observations from 45 prey species during the sampling period (Table 4).

Table 4: Species detected during visual surveys within Koeberg Nature reserve

	K1	K2	K6	K5	K7	K10	K12	K8	K11	K13
Alopochen aegyptiaca	1									
Anthobaphes violacea										1
Apus affinis					1	1			2	
Apus apus			1		1	1	1		2	
Apus caffer					1					
Cinnyris chalybeus	4	4		2		1	1		6	3
Circus maurus									1	
Cisticola tinniens			1				1			
Colius colius			1	1	1	2				1
Corvus albicollis							1			1
Corvus albus	8	2	1	1	2	1	1	2	4	1
Cossypha caffra	1	3	1	1	4	3	4	1	2	4
Elanus caeruleus	1						1			
Emberiza capensis						1	2			1
Estrilda astrild									1	
Euplectes capensis								2		
Falco rupicolus	1									
Himantopus himantopus							1			
Hirundo albigularis									1	
Hirundo rustica	2		3	2	4	2	2	3		4
Lamprotornis bicolor	1						2			1

33

Table 4: Continued

Species	K1	K2	K6	K5	K7	K10	K12	K8	K11	K13
Lamprotornis nitens										1
Lanius collaris	4	2	2		1	1			2	
Larus dominicanus							2			1
Macronyx capensis	2									
Motacilla capensis			1	1	1	1	2	2	1	1
Myrmecocichla formicivora		1								
Nectarinia famosa		1			1	1		1		
Oena capensis	4	1		1	3	4	2		4	
Onychognathus morio	1									
Pelecanus onocrotalus		2						1		
Phalacrocorax lucidus							2			
Ploceus capensis	1	1			1					
Prinia maculosa		5	1		3		2	3	3	1
Promerops cafer									1	
Pternistis capensis		1	1			1	5		2	1
Ptyonoprogne fuligula			1				1		1	
Pycnonotus capensis	3	2	4	7	8	9	8	8	5	4
Riparia cincta										1
Serinus canicollis	1						1			
Sphenoeacus afer							1			
Streptopelia capicola	2	1	1			2	1	3	2	2
Sturnus vulgaris										1
Tachymarptis melba					1				1	
Telophorus zeylonus	1							1		
Threskiornis aethiopicus		1							1	
Urocolius indicus			1			1		1	2	
Vanellus armatus	2									
Vanellus coronatus	2									
Zosterops virens	2			1		2	2	1		3

34

3.3.3 Sherman trap prey sampling results

Sherman trap sampling resulted in 412 captures from eight prey species during four surveys. All species were from the family Muridae and included; four species of mice, one species of rat, and three species of gerbil (Table 5).

Table 5: Numbers of small mammal prey by species and by site, trapped using Sherman Traps across four surveys within KPNR

	K1	K2	K5	K6	K7	K8	K10	K11	K12	K13
Acomys subspinosus	1				3	1				
Desmodillus auricularis							1			
Gerbilliscus afra	26	3		1	1		1		2	2
Gerbillurus paeba	3	4	1	13	5	12		2	2	4
Mus minutoides	1	1		1		1			1	1
Otomys irroratus	3			1	1					
Rhabdomys pumilio	11	73	21	76	42	28	8	27	9	16
Steatomys krebsii				1	1					

35

3.3.4 Trap array sampling

Trap array sampling resulted in 182 captures from 17 prey species during the sampling period. Prey species included one amphibian species, six reptile species including one snake species and nine small mammal species (Table 6).

Table 6: Prey animals, by species and by site, captured during trap array sampling across four surveys within KPNR

	K1	K2	K5	K6	K7	K8	K10	K11	K12	K13
Amphibians										
Tomopterna delalandii	1	3	1	2		11				1
Reptiles										
Meroles knoxii			1							
Afrogecko porphyreus					1					
Gerrhosaurus typicus		1			2					
Trachylepis capensis	6				3					
Trachylepis homalocephala	1				2	1	1	2	4	
Trachylepis variegata							1	1		
Rhinotyphlops lalandei							4			
Mammals										
Acomys subspinosus	2	2	1	9	4	7	2		1	7
Gerbillurus paeba					1					
Mus minutoides	3	1	2	5	2	6	1			1
Otomys irroratus			1							
Rhabdomys pumilio	1			1						
Steatomys krebsii		1			1	4				2
Dendromus melanotis	3		2			4	1			1
Dendromus mesomelas					1	1			1	
Myosorex varius	7	7		9	6	6	3	2	1	3

3.3.5 Measures of site-specific snake prey abundance

All snake species detected within KPNR include multiple prey types in their diet except for *Dasypeltis scabra*, which preys only on bird eggs. Lizards were the most important prey type for all species with the highest overall Community-wide Prevalence and Prey importance score (Table 7). Prey abundance measures varied greatly amongst cleared sites compared to undisturbed and burnt sites. There was no difference between prey abundance across vegetation types (one-way ANOVA test: $F_{2, 7} = 0.89$, p = 0.45, Figure 3). Prey abundance proxy measures ranged from 46.9 ± 9.11 (mean ± SE) for burnt sites, 40.1 ± 17.62 (mean ± SE) for cleared sites and 28.47 ± 1.58 (mean ± SE) for undisturbed sites

Table 7: Community-wide prevalence (CWP) and prey importance (PI) score for snake species across sites

Snake species	Lizards	Snakes	Amphibians	Birds	Mammals
Crotaphopeltis hotamboeia	1	0	1	0	1
Dasypeltis scabra	0	0	0	1	0
Homoroselaps lacteus	1	1	0	0	0
Lycodonomorphus inornatus	1	1	1	1	1
Naja nivea	1	1	1	1	1
Psammophis crucifer	1	1	1	0	0
Psammophis leightoni	1	1	0	0	1
Psammophylax rhombeatus	1	0	1	1	1
Pseudaspis cana	1	0	1	1	1
Community-wide Prevalence	0,89	0,56	0,67	0,56	0,67
Prey importance score	1,00	0,63	0,75	0,63	0,75

Table 8: Prey abundance proxy for snake communities at each ACO site

Site	Lizards	Snakes	Amphibians	Birds	Mammals	Total
K1	0,36	0,06	0,04	0,08	0,11	**65**
K2	0,06	0,07	0,12	0,05	0,11	**39**
K5	0,10	0,08	0,04	0,04	0,05	**30**
K6	0,04	0,05	0,08	0,04	0,15	**35**
K7	0,07	0,09	0,00	0,06	0,08	**30**
K8	0,08	0,08	0,43	0,06	0,10	**74**
K10	0,06	0,09	0,00	0,07	0,03	**24**
K11	0,09	0,05	0,00	0,09	0,04	**27**
K12	0,13	0,04	0,00	0,08	0,02	**28**
K13	0,00	0,02	0,04	0,06	0,06	**17**
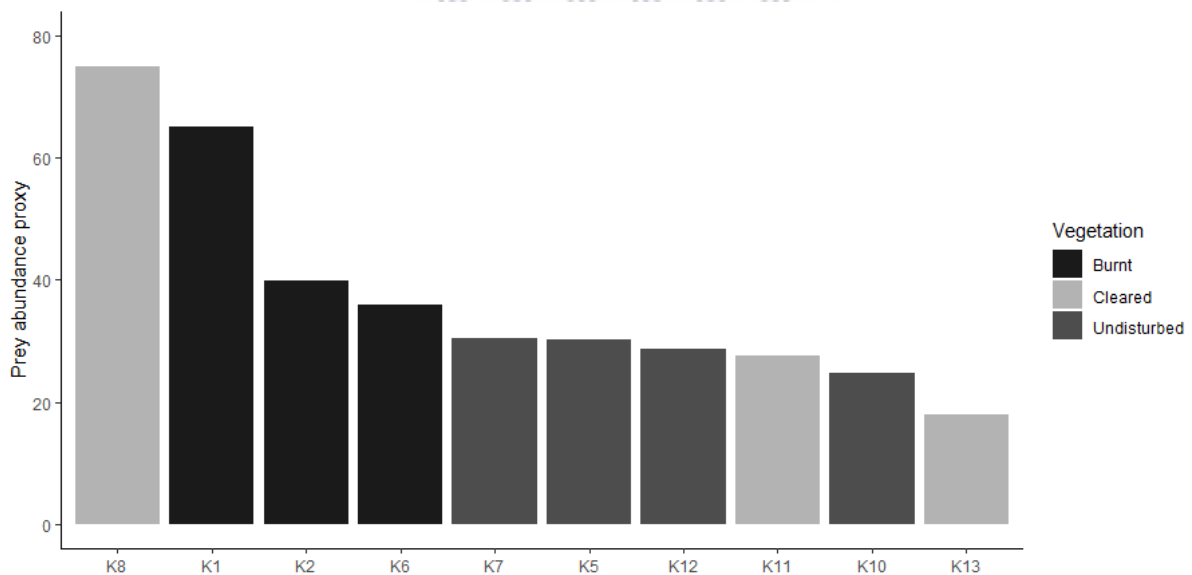
Figure 3: Prey abundance proxy for snake communities for sampling sites within KPNR. Index values account for detections of prey groups using multiple survey methods and account for the variation in diets by different species of snakes. The vegetation state is reflected for interest.

3.4 Predator communities

3.4.1 Camera trap results

Camera trap sampling resulted in 33 captures from six predator species during the sampling period (Table 9).

Table 9: Snake Predator species detected during camera trap surveys within Koeberg Nature reserve

	K1	K2	K5	K6	K7	K8	K10	K11	K12	K13
Caracal caracal		5	1		1					
Galerella pulverulenta			3				2	11		
Genetta genetta			3					1		1
Mellivora capensis							1	2		
Panthera pardus								1		
Vulpes chama	1									

3.4.2 Visual survey results

Visual surveys resulted in 43 detections of avian predators from seven predator species during the sampling period (Table 10).

Table 10: Snake Predator species detected during visual surveys within Koeberg Nature reserve

	K1	K2	K5	K6	K7	K8	K10	K11	K12	K13
Circus maurus						1				
Corvus albicollis									1	1
Corvus albus	8	2	1	1	2	2	1	4	1	1
Elanus caeruleus	1								1	
Falco rupicolous	1									
Lanius collaris	4	2		2	1		1	2		
Telophorus zeylonus	1									

39

3.5 Measures of site-specific snake predator abundance
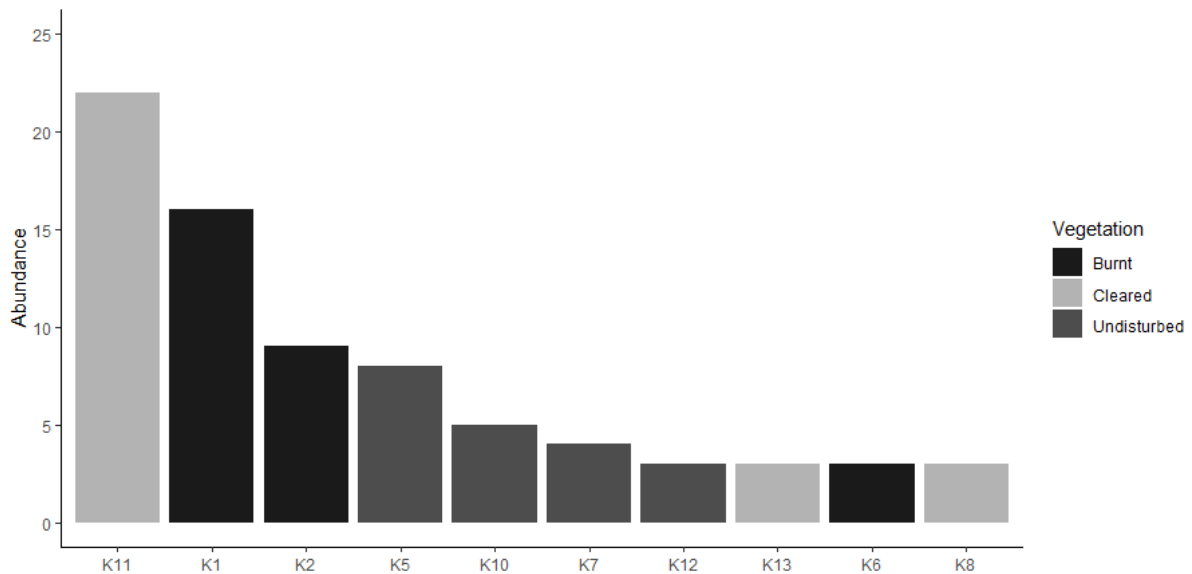
Figure 4: Predator abundance for snake communities for sampling sites within KPNR. Values account for detections of predator species using multiple survey methods. Vegetation state is reflected for interest.

The results for predator abundance demonstrated a similar trend to that of the prey abundance proxy measures with cleared sites having the highest variation in snake predator abundance (one-way ANOVA test: $F_{2,7} = 1.59$, $p = 0.27$, Figure 4). Predator abundance ranged from 7 ± 3.84 (mean $\pm$ SE) for burnt sites, 4 ± 1.21 (mean $\pm$ SE) for cleared sites and 2 ± 0.48 (mean $\pm$ SE) for undisturbed sites.

3.6 The effect of vegetation structure, prey abundance, and predator abundance on fine-scale variation in snake communities.

3.6.1 Community composition

Snake community composition was not significantly influenced by any of the five predictor variables (predator richness, predator abundance, prey richness, prey abundance, vegetation type) (Table 11). Of the five variables assessed, prey abundance had the most substantial overall effect, followed by prey richness, predator richness, predator abundance, and vegetation type. Despite having the most substantial community-level effect, univariate tests showed that no individual species contributed significantly to the effects of prey abundance on the multivariate snake community. While there was little evidence to suggest a strong influence of any of the explanatory variables on the snake community, individual snake species did respond differently to the predictor variables. Univariate tests showed that most individual species did not contribute significantly to the effects of any of the predictor variables. Eight of the ten individual species' responses to changes in vegetation type were negative, including that of the three species that indicated a significant response ($p < 0.05$). As expected, the two most abundant snake species, *Psammophylax rhombeatus* and *Psammophis crucifer* showed no significant response to any of the explanatory variables. All species that indicated a significant response to one or more explanatory variables were mainly positive, except for vegetation type, where all significant responses were negative. *Dasypeltis scabra* was the only species that responded significantly ($p > 0.05$) to both predator richness and abundance, while *Crotaphopeltis hotamboeia* showed a significant response to prey richness and prey abundance (Table 12).

41

3.6.2 Community metrics

All ten snake species detected during sampling were included in the community analysis to examine the response of the snake community's metrics (species richness, estimated species richness (Chao1), abundance, and biomass) to vegetation type, predators and prey abundance and species richness (Table 9). The null model was indicated as the optimal model in three snake community GLM analyses (species richness, estimated species richness, and abundance). The optimal model for the final metric, total biomass, included vegetation type, prey abundance, and prey species richness. In all the second and third-ranked models for the predictor variables, prey species richness and abundance were included (Table 11). The selection of the null models as the best-performing models suggests that the given predictor variables do not adequately explain the structure of snake communities within KPNR.

3.6.3 Individual species responses

Snake species were then assessed separately with GLM to determine the potential influence of the predictor variables on their abundance (Table 13). There was no significant effect from vegetation on any of the snake species. For five species (*Homoroselaps lacteus*, *Naja nivea*, *Psammophis crucifer*, *Psammophis leightoni*, *Pseudaspis cana*) the null model was the top-ranking model. Two species of snake (*Lycodonomorphus inornatus* and *Rhinotyphlops lalandei*) were only detected at one site (K10). Both species were negatively associated with predator abundance and positively associated with predator species richness. Predator species richness was positively associated with the abundance of *Dasypeltis scabra*. For the most abundant species across all sites, *Psammophylax rhombeatus*, prey abundance was the only variable in the top-performing model and was positively associated with the abundance of *P. rhombeatus*.

42

Table 11: The relationship between snake community metrics to vegetation type, predator, and prey species richness and abundance as described by generalized linear models with a Poisson distribution. The top 3 best ranking models are displayed with the number of parameters (df), log likelihood (loglik), AIC_c and AIC_c weight

Response variable	Terms in the optimal model	df	Loglik	AIC_c	AIC_c weight
	Null	1	-18.55	39.63	0.43
Snake species richness	Prey richness	2	-18.14	42.02	0.13
	Prey abundance	2	-18.26	42.21	0.12
	Null	1	-24.24	51.04	0.40
Snake estimated species richness	Prey richness	2	-23.78	53.34	0.13
	Prey abundance	2	-23.78	53.34	0.13
	Null	1	-28.26	59.01	0.41
Snake abundance	Prey Abundance	2	-27.79	61.31	0.13
	Prey richness	2	-28.21	62.14	0.09
	Vegetation type + Prey abundance + Prey richness	3	-245.57	307.52	0.91
Snake biomass	Vegetation + predator abundance + prey abundance + prey richness	3	-247.42	312.21	0.09
	Vegetation + Predator richness + prey abundance + prey richness	3	-248.79	317.00	0.01

Table 12: Summary of the multivariate analysis (manyglm) testing for the effects of each explanatory variable on snake community composition. The p values are given for the effect of variables at the community level. Estimates ± standard errors are indicated for each species contribution to the variance in the community composition. The community *p*-value indicates the effect of the response variable on the entire snake community. The sign of the estimate (positive or negative) indicates the direction of a species' response to the explanatory variable.

Explanatory variable	Community p-value	Species	p-value	Estimate ± se
Vegetation	0.884	*Crotaphopeltis hotamboeia*	**0.001**	**-1.48 ± 5.75**
		Dasypeltis scabra	0.65	-14.82 ± 5.75
		Homoroselaps lacteus	0.18	-1.09 ± 1.41
		Lycodonomorphus inornatus	**0.001**	**-1.48 ± 5.74**
		Naja nivea	0.38	-1.09 ± 1.22
		Psammophis crucifer	0.86	1.09 ± 0.33
		Psammophis leightoni	0.35	-1.09 ± 1.15
		Psammophylax rhombeatus	0.93	1.61 ± 0.26
		Pseudaspis cana	0.16	-0.41 ± 0.71
		Rhinotyphlops lalandei	**0.001**	**-1.48 ± 5.35**

Response variable	Community p-value	Species	p-value	Estimate ± se
Predator richness	0.329	*Crotaphopeltis hotamboeia*	0.39	-0.41 ± 0.66
		Dasypeltis scabra	**0.001**	**0.59 ± 0.29**
		Homoroselaps lacteus	0.10	0.43 ± 0.39
		Lycodonomorphus inornatus	0.42	0.11 ± 0.34
		Naja nivea	0.10	-0.41 ± 0.54
		Psammophis crucifer	0.41	-0.11 ± 0.13
		Psammophis leightoni	0.87	-0.04 ± 0.29
		Psammophylax rhombeatus	0.58	-0.05 ± 0.09
		Pseudaspis cana	0.73	0.11 ± 0.34
		Rhinotyphlops lalandei	0.42	0.11 ± 0.29

Table 12: Continued

Explanatory variable	Community p-value	Species	p-value	Estimate ± se
Predator abundance	0.398	*Crotaphopeltis hotamboeia*	0.08	-5.53 ± 17.48
		Dasypeltis scabra	**0.001**	**0.13 ± 0.07**
		Homoroselaps lacteus	0.22	0.07 ± 0.09
		Lycodonomorphus inornatus	0.32	-0.07 ± 0.13
		Naja nivea	0.08	-0.14 ± 0.18
		Psammophis crucifer	0.59	-0.02 ± 0.03
		Psammophis leightoni	0.97	-0.01 ± 0.07
		Psammophylax rhombeatus	0.93	0.01 ± 0.02
		Pseudaspis cana	0.66	0.03 ± 0.08
		Rhinotyphlops lalandei	0.31	-0.07 ± 0.11

Response variable	Community p-value	Species	p-value	Estimate ± se
Prey richness	0.301	***Crotaphopeltis hotamboeia***	**0.001**	**2.05 ± 18.57**
		Dasypeltis scabra	0.36	-0.15 ± 0.18
		Homoroselaps lacteus	0.08	0.17 ± 0.17
		Lycodonomorphus inornatus	0.29	0.14 ± 0.14
		Naja nivea	0.62	0.06 ± 0.15
		Psammophis crucifer	0.13	-0.08 ± 0.06
		Psammophis leightoni	0.26	0.10 ± 0.11
		Psammophylax rhombeatus	0.31	-0.04 ± 0.04
		Pseudaspis cana	0.64	-0.07 ± 0.18
		Rhinotyphlops lalandei	0.33	0.14 ± 0.12

45

Table 12: Continued

Explanatory variable	Community p-value	Species	p-value	Estimate ± se
Prey abundance	0.255	*Crotaphopeltis hotamboeia*	0.42	-0.05 ± 0.08
		Dasypeltis scabra	0.12	-0.07 ± 0.06
		Homoroselaps lacteus	0.45	0.02 ± 0.03
		Lycodonomorphus inornatus	0.23	-0.12 ± 0.09
		Naja nivea	0.18	-0.03 ± 0.05
		Psammophis crucifer	0.29	0.01 ± 0.01
		Psammophis leightoni	0.26	-0.03 ± 0.04
		Psammophylax rhombeatus	0.01	0.01 ± 0.01
		Pseudaspis cana	0.64	0.02 ± 0.03
		Rhinotyphlops lalandei	0.32	-0.12 ± 0.08
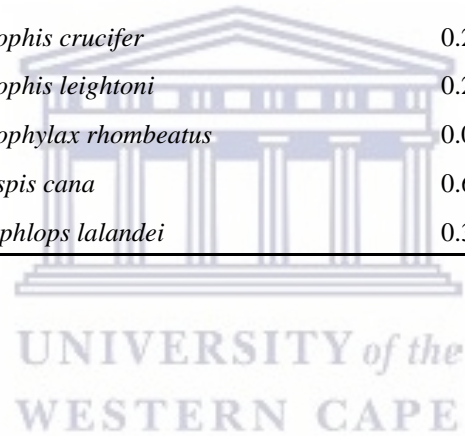
Table 13: The relationship between snake species abundance to vegetation type, predator and prey species richness, and abundance as described by generalized linear models with a Poisson distribution. The best ranking model is displayed for each species with the number of parameters (df), log likelihood (loglik), AIC_c and AIC_w

Snake species	Terms in the optimal model	df	Loglik	AIC_c	AIC_c weight
Crotaphopeltis hotamboeia	Prey richness	2	-1.31	8.29	0.50
Dasypeltis scabra	Predator richness	2	-5.84	17.35	0.26
Homoroselaps lacteus	Null	1	-5.22	12.87	0.25
Lycodonomorphus inornatus	Predator abundance + Predator richness + Prey richness	4	-1.49	19.23	0.16
Naja nivea	Null	1	-6.61	15.67	0.41
Psammophis crucifer	Null	1	-20.05	42.55	0.34
Psammophis leightoni	Null	1	-9.16	20.78	0.44
Psammophylax rhombeatus	Prey abundance	2	-19.62	45.57	0.25
Pseudaspis cana	Null	1	-6.61	15.65	0.47
Rhinotyphlops lalandei	Predator abundance + Predator richness	3	-1.63	13.29	0.24
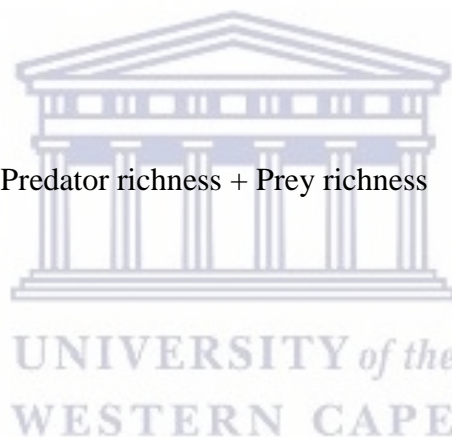
Chapter 4: Discussion

Koeberg Private Nature Reserve (KPNR) is home to snake communities that are not uniformly distributed across the reserve. I quantified the characteristics of snake communities and compared them across vegetation types using five community metrics. At a site scale, snake communities varied in species richness, biomass, and evenness to a lesser extent. Inter-site variation in snake communities was not well explained by my predictor variables. This is likely due to the varied responses of individual snake species to each community metric used in this study.

Ten of the 11 snakes predicted to occur within Koeberg (Bates et al. 2014) were detected during my study, with the expectation of *Dispholidus typus* (Boomslang). Only two of the ten snake species included in this study were detected across all ten ACO sites, namely *Psammophylax rhombeatus* and *Psammophis crucifer*. Several species were detected from undisturbed sites; *Crotaphopeltis hotamboeia*, *Naja nivea*, *Lycodonomorphus inornatus* and *Rhinotyphlops lalandei* all of these were represented by only one or two captures. The low recaptures recorded during my study and the results of the rarefaction curves and species richness estimator (Chao1) potentially indicate a larger snake population (Winck et al. 2007). This was mainly supported by the rarefaction curves, which did not reach an asymptote for most of the sites, which indicates that there could be other species at the sites that were not detected (Chao 1984). However, low detectability or high snake mobility could also explain the low recapture rates.

Snake communities are difficult to sample, and many studies on their communities do not detect all possible species within the area (Filippi and Luiselli 2007). Metrics such as species richness are essential for community studies as they provide baseline levels of understanding about the community composition in an area (Gotelli and Colwell 2001). I frequently

detected locally common species of snakes in KPNR, *Psammophylax rhombeatus* and *Psammophis crucifer,* and to a lesser extent *Psammophis leightoni* and *Dasypeltis scabra*, confirming these species as integral parts of the snake community. I also detected several species only represented by one or two individuals (*Crotaphopeltis hotamboeia*, *Naja nivea*, *Pseudaspis cana*, *Rhinotyphlops lalandei*). Some of these less common snake species have specialized life histories and occupy niches that make detecting them difficult (Durso and Winne 2011; Halliday and Blouin-Demers 2015). The presence of ecological specialists supports the notion that this ecosystem is heterogeneous as these species were only detected at specific sites (Cooper 2007).

Co-occurrence patterns in snake communities are often difficult to determine as patterns could result either from interspecific interactions or simply from differences in habitat preferences (Steen et al. 2014a). This is further confounded by the low detectability of specific snake species in different vegetation types (Miller et al. 2012). I attempted to explain both inter-site differences in snake communities and how individual snake species responded to different ecological processes for this study. Co-occurrence analysis indicated no specific patterns of coexistence for snake species, suggesting that any individual species were not shaping the structure of the snake communities in KPNR. The coexistence of species can be limited by ecological interactions such as interspecific competition, competition for habitats, and predator-prey interactions (Kneitel and Chase 2004). The importance of these ecological factors is often seen in communities with sympatric species in high abundance (Reinert 1984). In strandveld, even the most abundant species are not present in high numbers. This low abundance, coupled with the low metabolic rates seen in snake species (Greene 1997), can minimize the effects of these ecological factors. When considering the effects of the ecological interactions stated earlier, it becomes possible to assume that there would be no

true structure to these snake communities, indicating a random assortment of species at each site (Brose et al. 2003).

With my data, I found that only one of four community metrics could explain the snake community structure across the site. For the community analysis, total snake biomass was explained by vegetation type and prey availability (prey abundance and prey richness). Although snakes have lower metabolic rates compared to endotherms (Nagy 2005), their ecological success may be facilitated by food availability (Ford and Seigel 1989). Under the right conditions, high snake abundance may regulate prey populations (Nowak et al. 2008). Thus, the presence of a superior predator in a given habitat could decrease the prey availability for other competitors. The two most abundant snake species detected across my sites, *P. rhombeatus* and *P. crucifer* both prey on a variety of prey species and could be excluding other snake species from sites with low prey availability.

The composition of the snake communities at my sites are dominated by two species, *P. crucifer* and *P rhombeatus,* accounting for over 50% of all total captures, This pattern is consistent with the earlier snake community survey conducted in the reserve, which noted *P. crucifer* and *P rhombeatus* as the most abundant snakes in the reserve. The prevalence of these two species could indicate that they are better adapted to disturbed habitats, which favour these generalist species over specialist feeders. There were greater available food resources at burnt sites than at natural sites, noted by the prey abundance proxy measures. Likewise, cleared sites also showed high prey abundance, with one of the cleared sites (K8) indicating the greatest prey abundance measure overall. However, my results were unable to determine the reason for the prevalence of these two snake species across my sites. Apart from the variables that I measured there are likely additional factors accounting for the diversity and abundance of snake species in KPNR

50

The structure of ecological communities in many natural ecosystems is largely influenced by disturbances, which occur naturally or through anthropogenic activities. In these systems, disturbances alter the overall community structure, which in turn can affect community composition, and structure (Fakhry et al. 2020). Eight of the ten species with significantly lower abundance (n < 5) during the survey period, notably; *Crotaphopeltis hotamboeia, Naja nivea, Pseudaspis cana, Rhinotyphlops lalandei* were negatively associated with vegetation type. Undisturbed vegetation and landscapes with high vegetation cover often provide more resources, such as food, space, safe refuges, and better access to these resources. Theoretically, these areas can support a more extensive and diverse snake assemblage, as snake diversity is often negatively associated with increased disturbances (Piatti et al. 2019). Increased vegetation cover might also promote species co-occurrence by reducing competitive pressure associated with utilising similar resources. Nonetheless, patches of disturbed vegetation still contribute to the snake diversity in fragmented habitats. This was true, especially in burnt sites, which showed similar trends in snake abundance as natural sites but had significantly lower species richness.

The alteration of fynbos ecosystems in KPNR from burning and alien vegetation clearing favoured generalist-feeding snake species, namely, *P. crucifer* and *P rhombeatus,* by providing these species with increased food resource availability. The proliferation of these two species could further benefit the ecosystem by serving as prey to snake predators, such as *N. nivea*. Incidental records of *N. nivea* were detected more often than not at or near burned and natural sites along roads and the adjusted veld. While these records are mainly, incidentally, they shed light on the potential of these large-bodied snakes to occupy areas with increased snake abundance.

Studies on snake communities often highlight the role of prey availability in shaping snake communities (Weatherhead et al. 2010). For my study, I quantified prey species richness and

abundance to determine how they affected snake community structure. I developed a prey abundance index to assess snake community structure; this was done as I used multiple sampling methods to quantify prey abundance. I found that snake abundance was positively correlated with higher prey availability for *Psammophylax rhombeatus*, *Lycodonomorphus inornatus*, and *Crotaphopeltis hotamboeia*. The latter two species were only detected at a single site. While this does not allow for an accurate comparison between these species and their prey, it could indicate that these two species only occupy sites with increased prey availability. *Crotaphopeltis hotamboeia* is regarded as a frog specialist (Keogh et al. 2000). However, at the site they were detected, no frogs were captured during sampling. This could indicate that prey availability might not be driving *C. hotamboeia* occupancy within KPNR or that my amphibian sampling did not reflect underlying amphibian abundances.

Predators play a crucial role in ecosystems by altering the species richness and abundance of their prey species (Chalcraft and Resetarits 2003). The presence of predator species in an ecosystem can alter the structure of a community by consuming competitively superior prey species, thus altering the outcome of competitive interactions (Chalcraft and Resetarits 2003; Orrock et al. 2010). The three groups of snake predators observed in KPNR included reptiles, mammals, and birds and occurred across all sites. Raptors comprised the majority of snake predators observed during my study in terms of species richness and abundance and were mainly detected at disturbed sites. Aerial foragers, mainly raptors, generally show a preference for habitat edges and low vegetation cover, possibly reflecting their hunting strategies (Selås 2001; Stirnemann et al. 2015). Overall, there were no distinctive patterns in the species richness or abundance of snake predators across sites. While I detected more snake predators at disturbed sites, these sites were not statistically different from the undisturbed sites. The increased abundance of predators at disturbed sites could be attributed to the increased availability of prey species following disturbances of the natural food webs.

52

Koeberg Private Nature Reserve has seen increased levels of disturbances over the past years. In 2016 an uncontrolled fire burned through a portion of the reserve devastating the once natural strandveld vegetation. Additionally, management has been actively working to clear invasive *Acacia* species from the reserve. This has resulted in various patches of disturbed and undisturbed strandveld vegetation occurring throughout KPNR. While these types of disturbances are likely to benefit snake communities in the long run, through reduced competition, the initial effects can be quite devastating (Baker 1992, Morris et al. 2011). Small mammals and reptiles are among the first species to recolonise a patch following a disturbance. However, the reduction in vegetation cover following a disturbance oftentimes results in increased predation rates on these species. Non-snake predators (and increased predation by snakes) may suppress recolonization by these prey species resulting in an unstable food resource for snakes (Luiselli 2006b). In these conditions, snake species with a more generalist diet, as in the case of *P. rhombeatus*, may be better suited to persist, giving them a competitive advantage in strandveld.

Using ACOs to sample snakes minimises the concerns associated with daily survey methods (Fogarty and Jones 2003). For example, ACOs reduce the risk of snake species' mortality associated with trap array sampling. Sites can be left undisturbed for long periods, reducing the influence of human disturbances on snakes within the sites. The reduced activity at sites could also aid in detecting cryptic snake species or 'shy' species (Gray et al. 2010). Unfortunately, ACO sampling does not allow researchers to link temporal variables to snake detections as the exact capture time cannot be recorded.

My results confirm that snake communities can be diverse in heterogeneous habitats yet challenging to detect and sample (Durso et al. 2011). Several species that are known to KPNR likely went undetected due to differences in their life history and habitat preferences (Steen 2010). This can be noted with *D. typus*, which prefers a more arboreal lifestyle, while

53

none of the sampled sites had vegetation > 3 m in height. It is also possible that species went undetected due to inaccuracies in the distributional records on which I based my predictions.

Several changes could be used to enhance the trap array design and potentially yield a more accurate sample of the natural diversity of the snake community. For example, drift fencing could be optimized for sampling snakes in sandy soil and windy conditions. Additionally, future researchers could use different materials for constructing drift fences in KPNR. The low rigidity of the shade cloth meant that snakes could push past them and navigate around funnel traps (Greenberg et al. 1994).

Snake communities of the fynbos biome have not been sufficiently studied compared with other ecosystems such as grasslands (Lepš 2004) and forests (Paoletti et al. 2018). The coexistence of snake species is thought to be facilitated mainly through the partitioning of food resources (Reinert 1984), with vegetation type and predators influencing the degree of diet overlap, altering competition pressure (Luiselli 2006a). If snake communities are predicted to be structured by a combination of vegetation type, presence and abundance of predators, and prey availability, my results should have indeed provided more significant results than reported. Additional consideration should be taken towards the role of fires in fynbos ecosystems and their impact on snake community structure. If the co-occurrence of snake species is largely driven by dietary niche overlap then understanding how fires alter these ecosystems should provide further insight into the ecology of snake species in these ecosystems (Luiselli 2018).

Quantifying snake community responses requires understanding complex interactions between predators, prey, and the abiotic environment, which presents numerous challenges (Doherty et al. 2020). Firstly, it is difficult to quantify all sources of variability driving snake community structure. Despite my best efforts, including a sampling protocol explicitly

54

designed to capture all potential species, I predict that some of the associations between snake community structure and the presence and availably of prey, predators, and vegetation type observed here were probably driven by unmeasured environmental variability (Doherty et al. 2020). Furthermore, the effects of predators and prey on snake communities are likely to be context-dependent, so the effects of these factors on snake community structure are likely to depend on the abiotic and biotic processes at various scales, not accounted for in this study.

This study provides a foundation for future research that incorporates multiple sampling techniques and analysis into the assessments of snake diversity and a range of ecological factors. Researchers can institute more informative management plans with more information about the snake community in KPNR. In particular, multi-scale studies designed to detect or capture groups of snake species based on additional ecological variables could be more informative.

55
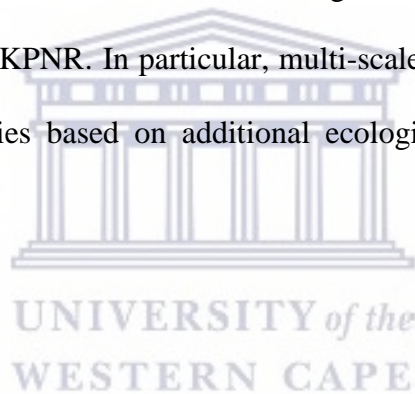
References

Alatalo, R. (1981). Problems in the measurement of evenness in ecology. *Oikos* 37(2): 199–204.

Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: A synthesis. *Ecology Letters* 6(12): 1109–1122.

Anderone, F., Luiselli, L. (2000). Are there shared general patterns of specific diversity, abundance, and guild structure in snake communities of tropical forests of Madagascar and continental Africa? *Revue d'écologie* 55(3): 215–239.

Araujo, M., Thuiller, W., Pearson, R. G. (2006). Climate warming and the decline of the amphibians and reptiles in Europe. *Journal of Biogeography* 33(10): 1712–1728.

Arnold, S. (1972). Species densities of predators and their prey. *The American Naturalist* 106(948): 220–236.

Baker, W. L. (1992). The landscape ecology of large disturbances in the design and management of nature reserves. *Landscape Ecology* 7(3): 181–194.

Barrull, J., Mate, I., Ruiz-Olmo, J., Casanovas, J. G., Gosàlbez, J., Salicrú, M. (2014). Factors and mechanisms that explain coexistence in a Mediterranean carnivore assemblage: An integrated study based on camera trapping and diet. *Mammalian Biology* 79(2): 123–131.

Bates, M.F., Branch, W. R., Bauer, A. M., Burger, M., Marais, J., Alexander, G., De Villiers, M. S. (2014). Atlas and red list of the reptiles of South Africa, Lesotho, and Swaziland. South Africa National Biodiversity Institute.

Bates, M. F., Little, I. T. (2013). Predation on the eggs of ground-nesting birds by *Dasypeltis scabra* (Linnaeus, 1758) in the moist highland grasslands of South Africa. *African*

Journal of Herpetology 62(2): 125–134.

Begg, C. M., Begg, K. S., Du Toit, J. T., Mills, M. G. L. (2003). Sexual and seasonal variation in the diet and foraging behaviour of a sexually dimorphic carnivore, the honey badger (*Mellivora capensis*). *Journal of Zoology* 260(3): 301–316.

Bellini, G. P., Giraudo, A. R., Arzamendia, V., Etchepare, E. G. (2015). Temperate snake community in South America: Is diet determined by phylogeny or ecology? *PLoS ONE* 10(5): 1–15.

Blonder, B. (2018). Hypervolume concepts in niche- and trait-based ecology. *Ecography* 41: 1441–1455.

Böhm, M., Collen, B., Baillie, J. E. M., Bowles, P., Chanson, J., Cox, N., Zug, G. (2013). The conservation status of the world's reptiles Kumlutas. *Biological Conservation* 157: 372–385.

Bonnet, X., Pearson, D., Ladyman, M., Lourdais, O., Bradshaw, D. (2002). ''Heaven'' for serpents? A mark–recapture study of tiger snakes (*Notechis scutatus*) on Carnac Island, Western Australia. *Austral Ecology* 27: 442–450.

Branch, W. R. (1998). Field Guide to Snakes and Other Reptiles of southern Africa. *Struik*

Breininger, D.R., Mazerolle, M.J., Bolt, M.R., Legare, M.L., Drese, J.H., Hines, J.E. (2012). Habitat fragmentation effects on annual survival of the federally protected eastern indigo snake. *Animal Conservation*. 15:361–368.

Bruckerhoff, L. A., Gido, K. B., Estey, M., Moore, P. J. (2021). Disentangling effects of predators and landscape factors as drivers of stream fish community structure. *Freshwater Biology* 66(4): 656–668.

Buckley, R. C. (2015). Grand challenges in conservation research. *Frontiers in Ecology and*

Evolution 3(11): 1–4.

Bury, B. R., Corn, P. S. (1987). Evaluation of pitfall trapping in Northwestern forests: Trap arrays with drift fences. *The Journal of Wildlife Management* 51(1) 112 –119.

Chaudhary, A., Pfister, S., Hellweg, S. (2016). Spatially explicit analysis of biodiversity loss due to global agriculture, pasture and forest land use from a producer and consumer perspective. *Environmental Science and Technology* 50(7): 3928–3936.

Cairns J, Moerman F, Fronhofer EA, Altermatt F, Hiltunen T. (2020). Evolution in interacting species alters predator life-history traits, behaviour and morphology in experimental microbial communities. *Proceedings of the Royal Society B* 287: 20200652.

Campbell, E. W., Yackel Adams, A. A., Converse, S. J., Fritts, T. H., Rodda, G. H. (2012). Do predators control prey species abundance? An experimental test with brown treesnakes on Guam. *Ecology* 93(5): 1194 – 1203.

Campbell, H. W., Christman, S.P. (1982). Field techniques for herpetofaunal community analysis. *Herpetological Communities*. 193-200.

Capizzi, D., Luiselli, L., Capula, M., Rugiero, L. (1995). Feeding habits of a Mediteranean community of snakes in relation to prey availability. *Revue d'Ecologie: Terre et La Vie* *50*(4): 353–363.

Cardinale, B. J., Weis, J. J., Forbes, A. E., Tilmon, K. J., Ives, A. R. (2006). Biodiversity as both a cause and consequence of resource availability: A study of reciprocal causality in a predator-prey system. *Journal of Animal Ecology* 75(2): 497–505.

Cavallini, P., Nel, J. A. J. (1990). The feeding ecology of the Cape grey mongoose, *Galerella pulverulenta* (Wagner 1839) in a coastal area. *African Journal of Ecology* 28: 123–130.

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters* 12(7): 693–715.

Chalcraft, D. R., Resetarits, W. J. (2003). Predator Identity and Ecological Impacts: Functional Redundancy or Functional Diversity? *Ecology* 84(9): 2407–2418.

Chao, A. (1984) Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11: 265–270.

Chase, J. M., Leibold, M. A., Downing, A, Shurin, J. B. (2000). Effects of productivity, herbivory and plant species turnover in grassland food webs. *Ecology* 81: 2485–2497.

Chave, J. (2004). Neutral theory and community ecology. *Ecological letters* 7(3): 241–253.

Clements, F. E., (1936). Nature and strucutre of the climax. *Journal of Ecology* 24: 252–284.

Colorado Zuluaga, G. (2015). How ecological communities are structured: A review on ecological assembly rules. *Revista EIA* 12(24): 27–53.

Coombs, G. (2016). Quantifying predation pressure and the protective role of sheltered basking sites for small snakes in South Africa. *Phyllomedusa* 15(2): 155–162.

Cooper, W.E., Jr., Secor, S. (2007). Strong response to anuran chemical cues by an extreme dietary specialist, the eastern hog-nosed snake (*Heterodon platirhinos*). *Canadian Journal of Zoology* 85:619–625.

Costa-Pereira, R., Rudolf, V. H. W., Souza, F., Araujo, M. S. (2018). Drivers of individual niche variation in coexisting species. *Journal of Animal Ecology* 87: 1452–1464.

Cottone, A. M., Bauer, A. M. (2008). Prey excavation by *Psammophylax rhombeatus rhombeatu*s (Colubridae: Psammophiinae) from South Africa. *Herpetological Bulletin* (103): 11–15.

Cottone, A. M., Bauer, A. M. (2010). Sexual dimorphism, diet, reproduction, and their

geographic variation in sympatric Psammophiids, *Psammophis crucifer* and *Psammophylax rhombeatus rhombeatus*, from southern Africa. *Copeia* 2010(4): 578–590.

Cox, C. L., Farrar, E. S., Hey, J. D., Morrill, M. C. (2009). Cover object usage among an assemblage of Iowa snakes. *Herpetological Conservation and Biology 4*(1), 80–84.

Cox, N., Young, B. E., Bowles, P., Fernandez, M., Marin, J., Rapacciuolo, G., Böhm, M., Brooks, T. M., Hedges, S. B., Hilton-Taylor, C., Hoffmann, M., Jenkins, R. K. B., Tognelli, M. F., Alexander, G. J., Allison, A., Ananjeva, N B., Auliya, M., Avila, L. J., Chapple, D. G., Cisneros-Heredia, D. F., Cogger, H. G., Colli, G. R., de Silva, A., Eisemberg, C. C., Els, J., Fong, A. G., Grant, T. D., Hitchmough, R. A., Iskandar, D. T., Kidera, N., Martins, M., Meiri, S., Mitchell, N J., Molur, S., Nogueira, C. C., Ortiz, J C., Penner, J., Rhodin, A. G.J., Rivas, G. A., Rödel, M. O., Roll, U., Sanders, K. L., Santos-Barrera, G., Shea, G. M., Spawls, S., Stuart, B. L., Tolley, K. A., Trape, J.., Vidal, M. A., Wagner, P., Wallace, B. P., Xie, Y. (2022). A global reptile assessment highlighted shared conservation needs of tetrapods. *Nature* 605(7909): 285–290.

Cramer, M. J., Willig, M. R. (2005). Habitat heterogeneity, species richness and null models. *Oikos* 108: 209–218

Doherty, T. S., Balouch, S., Bell, K., Burns, T. J., Feldman, A., Fist, C., Garvey, T. F., Jessop, T. S., Meiri, S., Driscoll, D. A. (2020). Reptile responses to anthropogenic habitat modification : A global meta-analysis. *Global Ecology and Biogeography* 29: 1265–1279

Durso, A. M., Willson, J. D., Winne, C. T. (2011). Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes. *Biological Conservation* 144(5): 1508–1515.

Dyer, B. M. (1996). Predation by snakes on seabirds at three South African Islands. *South African Journal of Marine Science* 17: 309–313.

Edgehouse, M., Latta IV, L. C., Brodie, E. D., Brodie, E. D. (2014). Interspecific aggression and habitat partitioning in garter snakes. *PLoS ONE* 9(1): 1–5.

Elton, C. S. (1946). Competition and the structure of animal communities. *Journal of Animal Ecology* 15(1): 54–68.

Englund, G., Leonardsson, K. (2008). Scaling up the functional response for spatially heterogeneous systems. *Ecology Letters* 11: 440–449.

Eskew, E. A., Todd, B. D. (2017). Too cold, too wet, too bright, or just right? Environmental predictors of snake movement and activity. *Copeia* 105(3): 584–591.

Eskom Holdings SOC Limited. (2014). Management plan for the Koeberg Nature Reserve, Western Cape, South Africa, 1–30.

Evans, M. R. (2012). Modelling ecological systems in a changing world. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367(1586): 181–190.

Faeth, S. H., Warren, P. S., Shochat, E., Marussich, W. A. (2005). Trophic Dynamics in Urban Communities. *BioScience* 55(5): 399–407.

Fakhry, A., Khazzan, M. M., Aljedaani, G. S. (2020). Impact of disturbance on species diversity and composition of *Cyperus conglomeratus* plant community in southern Jeddah, Saudi Arabia. *Journal of King Saud University- Science* 32(1): 600–605.

Finch, D. M. (1989). Habitat use and habitat overlap of riparian birds in three elevational zones. *Ecology* 70: 866–880.

Ford, N. B., R. A. Seigel. 1989. Phenotypic plasticity in reproductive traits: Evidence from a viviparous snake. *Ecology* 70: 1768–1774.

61

Forgus, J. (2018). Functional importance of snakes in a strandveld ecosystem. Unpublished Masters thesis. Biodiversity and Conservation Biology Department. University of the Western Cape.

Filippi, E. Luiselli, L. (2007). Non-random seasonal variation in the structure of a Mediterranean snake community. *Web Ecology* 7: 40–46.

França, F. G. R., Araújo, A. F. B. (2007). Are there co-occurrence patterns that structure snake communities in Central Brazil? *Brazilian Journal of Biology* 67(1): 33–40.

Franklin, J. (2010). Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions* 16(3): 321–330.

Gartner, G. E. A., Greene, H. W. (2008). Adaptation in the African egg-eating snake: A comparative approach to a classic study in evolutionary functional morphology. *Journal of Zoology* 275(4): 368–374.

Giam, X. (2017). Global biodiversity loss from tropical deforestation. *Proceedings of the National Academy of Sciences of the Untied Staes of America* 114(23): 5775–5777.

Gleason, H. A. (1926) The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53: 7–26.

Glen, A. S., Dickman, C. R. (2005). Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biological Reviews* 80: 387–401.

Gotelli, N. J., Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecological Letters* 4: 379–391.

Götzenberger, L. et al. 2012. Ecological assembly rules in plant communities – approaches, patterns and prospects. *Biolological Reviews* 87: 111–127.

Greenberg, C. H., Neary, D. G. and Harris, L. D. (1994): A comparison of herpetofaunal sampling effectiveness of pitfall, single-ended, and double-ended funnel traps used with drift fences. *Journal of Herpetology* 28: 319–324.

Grinnell, J, (1917). The niche-relationship of the California Thrasher. *The Auk* 34: 427–433.

Harrison, S., Cornell, H. (2008). Toward a better understanding of the regional causes of local community richness. *Ecology Letters* 11(9): 969–979.

Hubbell, S. P. (2001). A Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ.

Hubbell, S. P., Ahumada, J. A., Condit, R., Foster, R. B. (2001). Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research* 16(5): 859–875.

Hutchinson, G. E. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist* 93: 145–159.

Jacobsen, N. H. G., Randall, R. M. (2013). Survey of reptiles in the Wilderness section of the Garden Route National Park, South Africa. *Herpetology Notes* 6(1): 209–217.

Karameta, E., Papadopoulos, V. V., Pafilis, P. (2015). First record of ophiophagy in the roughtail rock agama (*Stellagama stellio*): One of the most rare feeding behaviors among european lizards. *Herpetology Notes* 8(4): 111–113.

Kelly, C. M. R., Barker, N. P., Villet, M. H., Broadley, D. G., Branch, W. R. (2008). The snake family Psammophiidae (Reptilia: Serpentes): phylogenetics and species delimitation in the African sand snakes (Psammophis Boie, 1825) and allied genera. *Molecular Phylogenetics and Evolution* 47: 1045–1060.

Keogh, J. S., Branch, W. R., Shine, R. (2000). Feeding ecology, reproduction and sexual

dimorphism in the colubrid snake *Crotaphopeltis hotamboeia* in southern Africa. *African Journal of Herpetology* 49(2): 129–137.

Kjoss VA, Litvaitis JA. (2001). Community structure of snakes in a human-dominated landscape. *Biological Conservation* 98: 285–292.

Kneitel, J. M., Chase, J. M. (2004). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecological letters* 7: 69–80.

Krupek, A., Gaertner, M., Holmes, P. M., Esler, K. J. (2016). Assessment of post-burn removal methods for *Acacia saligna* in Cape Flats Sand Fynbos, with consideration of indigenous plant recovery. *South African Journal of Botany* 105: 211–217.

Kusamba, C., Resetar, A., Wallach, V., Lulengo, K., Nagy, Z. T. (2013). Mouthful of snake: An African snake-eater's (*Polemon fulvicollis graueri*) large typhlopid prey. *Herpetology Notes* 6(1): 235–237.

Lawson, L., Moyer, D. (2008). Within and between-site distribution of frog species on the Udzungwa plateau, Tanzania. *African Journal of Herpetology* 57(2): 93–102.

Lawton J. H. (1999). Are there general laws in ecology? *Oikos* 84(2): 177–192.

Layloo, I., Smith, C., Maritz, B. (2017). Diet and feeding in the Cape Cobra , *Naja nivea*. *African Journal Of Herpetology* 66(2): 147–153.

Lepš, J. (2004). Variability in population and community biomass in a grassland community affected by environmental productivity and diversity. *Oikos* 107(1): 64–71.

Lima, S. L. (2002). Putting predators back into behavioral predator–prey interactions. *Trends in Ecology Evolution* 17(2): 70–75.

Lovich, J., Drost, C., Monatesti, A. J., Casper, D., Wood, D. A., Girard, M. (2010). Reptilian prey of the sonora mud turtle (*Kinosternon sonoriense*) with comments on saurophagy

and ophiophagy in North American turtles, *The Southwestern Naturalist* 55(1): 135–138.

Luiselli, Luca. (2003). Do snakes exhibit shifts in feeding ecology associated with the presence or absence of potential competitors? A case study from tropical Africa. *Canadian Journal of Zoology* 81(2): 228–236.

Luiselli, Luca. (2006). Resource partitioning and interspecific competition in snakes: The search for general geographical and guild patterns. *Oikos* 114(2): 193–211.

Luiselli, Luca, Filippi, E. (2006). Null models, co-occurrence patterns, and ecological modelling of a Mediterranean community of snakes. *Amphibia Reptilia* 27(3): 325–337.

Luiselli, L. (2006). Testing hypotheses on the ecological patterns of rarity using a novel model of study: Snake communities worldwide. *Web Ecology* 6: 44–58.

Schwartz, M. W., Brigham, C. A., Hoeksema, J. D., Lyons, K. G., Mills, M. H., van Mantgem, P. J. (2000). Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* 122: 297–305.

MacArthur, R. H., Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101: 377–385.

MacArthur, R. H., MacArthur, J. W. (1961). On bird species diversity. *Ecology* 42: 594–598.

Mannocci, L., Monestiez, P., Bolaños-jiménez, J., Dorémus, G., Jeremie, S., Laran, S., Rinaldi, R., Canneyt, O. V., Ridoux, V. (2013). Megavertebrate communities from two contrasting ecosystems in the western tropical Atlantic. *Journal of Marine Systems* 111–112.

Maritz, B., Alexander, G. J. (2007). Herpetofaunal Utilisation of riparian buffer zones in an agricultural landscape near Mtunzini, South Africa. *African Journal of Herpetology* 56(2): 163–169.

Maritz, B., Alexander, G. J. (2012). Population density and survival estimates of the African viperid, *Bitis schneideri*. *Herpetologica* 68(2): 195–202.

Maritz, B., Alexander, G. J., and Maritz, R. (2019). The underappreciated extent of cannibalism and ophiophagy in African cobras. *Ecology* 100(2): 1–3

Maritz, B., Scott, S. L. (2010). Assessing the threat of avian predation on a small viperid snake. *African Zoology* 45(10): 309–314.

Maritz, R., Conradie, W., Sardinha, C. I., Peto, A., Chechene, A. H. D., Maritz, B. (2019). Ophiophagy and cannibalism in African vine snakes (Colubridae: *Thelotornis*). *African Journal of Ecology* 58(3): 543–547.

Maritz, RA., Maritz, B. (2020). Sharing for science: high-resolution trophic interactions revealed rapidly by social media. *PeerJ* 8: e9485.

Martín, J., López, P. (1996). Avian Predation on a Large Lizard (*Lacerta lepida*) Found at Low Population Densities in Mediterranean Habitats: An Analysis of Bird Diets. *Copeia* 1996(3): 722–726.

Martins, M. (1996). Defensive tactics in lizards and snakes: the potential contribution of the Neotropical fauna. in Del Claro, K. (ed.), Anais do XIV Encontro Anual de Etologia. Sociedade Brasileira de Etologia, Universidade Federal de Uberlandia, Brasil. 185–199

Masters, R.E., Lochmiller, R.L., McMurry, S.T. and Bukenhofer, G.A. (1998) Small mammal response to pine-grassland restoration for red-cockaded woodpeckers. *Wildlife Society Bulletin* 26: 148–158.

Masterson, G. P. R., Maritz, B., Alexander, G. J. (2008). Effect of fire history and vegetation structure on herpetofauna in a South African grassland. *Applied Herpetology* 5: 129–143.

66

McCauley, D. J., Keesing, F., Young, T. P., Allan, B. F., Pringle, R. M. (2006). Indirect effects of large herbivores on snakes in an African savanna. *Ecology* 87(10): 2657–2663.

McGill, B. J., Enquist, B. J., Weiher, E., Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecology and Evolution* 21: 178–185

Mehring, M. Bernard, B., Hummel, D. Liehr, S., Lux, A. (2017). Halting biodiversity loss: how social–ecological biodiversity research makes a difference. *International Journal of Biodiversity Science, Ecosystem Services* and *Management* 13(1): 172–180.

Millennium Ecosystem Assessment. (2005). Ecosystems and human well-being: synthesis. Washington, DC: Island Press.

Mohseni, M. R., Pashaei Rad, S. (2021). The effect of edaphic factors on the distribution and abundance of ants (Hymenoptera: Formicidae) in Iran. *Biodiversity Data Journal* 9: e54843.

Morris, D. W., Kingston, S. R. (2002). Predicting future threats to biodiversity from habitat selection by humans. *Evolutionary Ecology Research* 4: 787–810.

Miller, D. A. W., Weir, L. A., McClintock, B. T., Grant, E. H. C., Bailey, L.L. and Simons, T. R. (2012). Experimental investigation of false positive errors in auditory species occurrence surveys. *Ecological Applications* 22: 1665–1674.

Mukundamago, M. (2016). Restoration of Cape Flats Sand Fynbos : The significance of pre-germination treatments and moisture regime.Unpublished Masters Thesis, Faculty of AgriSciences. Stellenbosch University

Nagy K. A. (2005). Field metabolic rate and body size. *The Journal of Experimental Biology* 208(9): 1621–1625

Nowak EM, Theimer TC, Schuett GW. (2008). Functional and numerical responses of

predators: Where do vipers fit in the traditional paradigms? *Biological Reviews* 83: 601–620.

Oksanen, J. (2017). Vegan: ecological diversity. *R Package Version 2.4-4*, *1*, 11. Retrieved from https://cran.r-project.org/package=vegan

Orrock, J. L., Dill, L. M., Sih, A., Grabowski, J. H., Peacor, S. D., Peckarsky, B. L., Preisser, E. L., Vonesh, J. R., Werner, E. E. (2010). Predator effects in predator-free space: the remote effects of predators on prey. *The Open Ecology Journal* 3: 22–30.

Ortega, J. C. G., Figueiredo, B. R. S., da Graça, W. J., Agostinho, A. A., Bini, L. M. (2020). Negative effect of turbidity on prey capture for both visual and non-visual aquatic predators. *Journal of Animal Ecology* 89: 2427–2439.

Paine, C. E. T., Deasey, A., Duthie, A. B. (2018). Towards the general mechanistic prediction of community dynamics. *Functional Ecology* 9: 1681–1692.

Paoletti, A., Darras, K., Jayanto, H., Grass, I., Kusrini, M., Tscharntke, T. (2018). Amphibian and reptile communities of upland and riparian sites across Indonesian oil palm, rubber and forest. *Global Ecology and Conservation* 16: e00492.

Perkins, M. W., Cloyed, C. S., Eason, P. K. (2020). Intraspecific dietary variation in niche partitioning within a community of ecologically similar snakes. *Evolutionary Ecology* 34(6): 1017–1035.

Piatti, L., Rosauer, D. F., Nogueira, C. D. C., Strussmann, C., Lúcia, V., Martins, M. (2019). Snake diversity in floodplains of central South America : Is flood pulse the principal driver? *Acta Oecologica* 97(4): 34–41.

Portillo, F., Stanley, E. L., Branch, W. R., Conradie, W., Rödel, M. O., Penner, J., Greenbaum, E. (2019). Evolutionary history of burrowing asps (Lamprophiidae: Atractaspidinae) with emphasis on fang evolution and prey selection. *PLoS ONE* 14(4):

1–32.

Rainsford, F. W., Kelly, L. T., Leonard, S. W. J., Bennett, A. F. (2020). Post-fire development of faunal habitat depends on plant regeneration traits. *Austral Ecology* 45: 800–812.

Ramadoss, A., Poyyamoli, G. (2011). Biodiversity conservation through environmental education for sustainable development - a case study from Puducherry, India. *International Electronic Journal of Environmental Education* 1(2): 97–111.

Reading, C. J., Luiselli, L. M., Akani, G. C., Bonnet, X., Amori, G., Ballouard, J. M., Filippi, E., Naulleau, G., Pearson, D., Rugiero, L. (2010). Are snake populations in widespread decline? *Biology letters* 6: 777–780.

Reichenbach, N. G., Dalrymple, G. H. (1980). On the criteria and evidence for interspecific competition in snakes. *Journal of Herpetology* 14(4): 409–412.

Rosenzweig, M. L., Winakur, J. (1969). Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* 50(4): 558–572.

Mucina, L., Rutherford, M. C. (2006). The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria

Reinert, H. K. (1984). Habitat Varition Within Sympatric Snake Populations. *Ecology* 65(5): 1673–1682.

Ricklefs, R. E., (1987). Community diveristy: relatives roles of local and regional processes. *Science* 235: 167–171.

Ricklefs R. E. 2008. Disintegration of the ecological community. *American Naturalist* 172:741–750.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., Böhm, M.,

Castro-Herrera, F., Chirio, L., Collen, B., Colli, G. R., Dabool, L., Das, I., Doan, T. M., Grismer, L. L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., Lewin, A., Martins, M., Maza, E., Meirte, D., Nagy, Z. T., Nogueira, C. C., Pauwels, O. S. G., Pincheira-Donoso, D., Powney, G. D., Sindaco, R., Tallowin, O. J. S., Torres-Carvajal, O., Trape, J. F., Vidan, E., Uetz, P., Wagner, P., Wang, Y., Orme, C. D. L., Grenyer, R., Meiri, S. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature ecology and evolution* 1: 1667–1682.

Rose, G. A., Leggett, W. C. (1990). The importance of scale to predator-prey spatial correlations: an example of atlantic fishes *Ecology* 71(1) 33–43.

Rowland, J., Nottidge, B., Ferguson, D., Mathieson, M. (2012). Predation by an eastern brownsnake *Pseudonaja textilis* on a common death adder *Acanthophis antarcticus* (serpentes: Elapidae), *Herpetofauna* 42(1): 28–37.

Sasaki, K., Lesbarrères, D., Beaulieu, C. T., Watson, G., Litzgus, J. (2016). Effects of a mining-altered environment on indivudal fitness of amphibians and reptiles. *Ecosphere:* 7(6) e01360

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science* 185: 27–39

Selås, V. (2001). Predation on reptiles and birds by the common buzzard, *Buteo buteo*, in relation to changes in its main prey, voles. *Canadian Journal of Zoology* 79(11): 2086–2093.

Shackelford, N., Standish, R. J., Ripple, W., Starzomski, B. M. (2018). Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. *Conservation Biology* 32(3): 672–684.

Shine, R., Branch, W. R., Webb, J. K., Harlow, P. S., Shine, T., Keogh, J. S. (2007). Ecology

of cobras from southern Africa. *Journal of Zoology* 272(2): 183–193.

Shine, R., Branch, W. R., Webb, J. K., Harlow, P. S., Shine, T. (2017). Sexual Dimorphism , Reproductive Biology, and Dietary Habits of Psammophiine Snakes (*Colubridae*) from Southern Africa. *Copeia* 2006(4): 650–664.

Shine, Richard, Harlow, P. S., Branch, W. R., Webb, J. K. (1996). Life on the lowest branch: Sexual dimorphism, diet, and reproductive biology of an African twig snake, *Thelotornis capensis* (Serpentes, Colubridae). *Copeia* 1996(2): 290–299.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. (1985). Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16: 269–311.

Simberloff, D. and Dayan, T. (1991). The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* 22: 115–143.

Soberón, J., and Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2: 1–10.

Steen, D. A., Mcclure, C. J. W., Brock, J. C., Craig Rudolph, D., Pierce, J. B., Lee, J. R., Jeffrey Humphries, W., Gregory, B. B., Sutton, W. B., Smith, L. L., Baxley, D. L., Stevenson, D. J., Guyer, C. (2014). Snake co-occurrence patterns are best explained by habitat and hypothesized effects of interspecific interactions. *Journal of Animal Ecology* 83: 286–295.

Steen, D. A., Mcclure, C. J. W., Sutton, W. B., Craig Rudolph, D., Pierce, J. B., Lee, J. R., Smith, L. L., Gregory, B. B., Baxley, D. L., Stevenson, D. J., Guyer, C. (2014). Copperheads are common when kingsnakes are not: Relationships between the abundance of a predator and one of their prey. *Herpetologica* 70(1): 69–76.

Stirnemann, I. A., Ikin, K., Gibbons, P., Blanchard, W., Lindenmayer, D. B. (2015).

71

Measuring habitat heterogeneity reveals new insights into bird community composition. *Oecologia* 177(3): 733–746.

Taft, J.M., Martix, B., Tolley, K.A. (2021). Stable climate corridors promote gene flow in the Cape sand species complex (Psammophiidae). *Zoologica Scripta* 1–18.

Tews, J., Brose, U., Grimm. V., Tielborger, K., Wichmann, M. C., Schwager, M., Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31: 79–92.

Thébault, E., Loreau, M. (2005). Trophic interactions and the relationship between Species diversity and ecosystem stability. *The American Naturalist* 166(4): 95–114.

Tolley, K. A., Alexander, G. J., Branch, W. R., Bowles, P., Maritz, B. (2016). Conservation status and threats for African reptiles. *Biological Conservation* 204: 63–71.

Tolley, K. A., Weeber, J., Maritz, B., Verburgt, L., Bates, M. F., Conradie, W., Hofmeyr, M. D., Turner, A. A., da Silva, J. M., Alexander, G. J. (2019). No safe haven: Protection levels show imperilled South African reptiles not sufficiently safe-guarded despite low average extinction risk. *Biological Conservation* 233: 61–72.

Triska, M. D., Craig, M. D., Stokes, V. L., Pech, R. P., Hobbs, R. J. (2017). Conserving reptiles within a multiple-use landscape: determining habitat affiliations of reptile communities in the northern jarrah forest of south-western Australia. *Australian Journal of Zoology* 65(2017): 21–32.

Tulloch, A. I. T., Hagger, V., Greenville, A. C. (2020). Ecological forecasts to inform near-term management of threats to biodiversity. *Global Change Biology* 2020(26): 5816–5828.

Vellend, M. (2010). Conceptual synthesis in community ecology. *Quarterly Review of Biology* 85(2): 193–206

72

Vitt, L. J., Pianka, E. R., Cooper, W. E. Jr., Schwenk, K. (2003). History and the global ecology of squamate reptiles. *American Naturalist* 162: 44–60.

Voss, R. S., Jansa, S. A. (2012). Snake-venom resistance as a mammalian trophic adaptation: Lessons from didelphid marsupials. *Biological Reviews* 87(4): 822–837.

Wang, C., Qi, S. (2018). Spatial dynamics of a predator-prey system with cross diffusion. *Chaos, Solitons and Fractals* 107: 55–60.

Weatherhead, P. J., Carfagno, G. L. F., Sperry, J. H., Brawn, J. D. Robinson, S. K. (2010). Linking snake behavior to nest predation in a Midwestern bird community. *Ecological Applications* 20(1): 234–241.

Webb, J. K., Branch, W. R., Shine, R. (2001). Dietary habits and reproductive biology of typhlopid snakes from southern Africa. *Journal of Herpetology* 35(4): 558–567.

Whelan, C. J., Şekercioğlu, Ç. H., Wenny, D. G. (2015). Why birds matter: From economic ornithology to ecosystem services. *Journal of Ornithology* 156: 227–238.

Willig, M. R., Kaufman, D. M. Stevens, R. D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34: 273–309

Winck, G. R., dos Santos, T. G., Cechin, S. Z., (2007). Snake assemblage in a disturbed grassland environment in Rio Grande do Sul State, southern Brazil: population fluctuations of *Liophis poecilogyrus* and *Pseudablabes agassizii*. *Annales Zoologici Fennici* 44(5): 321–332.

Zipkin, E. F., DiRenzo, G. V., Ray, J. M., Rossman, S., Lips, K. R. (2020). Tropical snake diversity collapses after widespread amphibian loss. *Science* 367: 814–816.

Appendices

Appendix 1: Camera trap records for snake communities across all sites

Site	Date	Time	Latitude	Longitude	*Species*	Common name
K1	20/05/2018	03:05	-33,662291	18,453943	*Vulpes chama*	Cape Fox
K2	19/05/2018	23:53	-33,651422	18,447061	*Caracal caracal*	Caracal
K2	14/12/2018	21:36	-33,651422	18,447061	*Caracal caracal*	Caracal
K2	17/12/2018	21:47	-33,651422	18,447061	*Caracal caracal*	Caracal
K2	17/12/2018	22:00	-33,651422	18,447061	*Caracal caracal*	Caracal
K2	17/12/2018	00:20	-33,651422	18,447061	*Caracal caracal*	Caracal
K2	10/04/2019	03:41	-33,651422	18,447061	*Caracal caracal*	Caracal
K2	11/04/2019	00:25	-33,651422	18,447061	*Caracal caracal*	Caracal
K5	22/06/2018	14:45	-33,651469	18,439825	*Galerella pulverulenta*	Cape Grey mongoose
K5	22/06/2018	15:30	-33,651469	18,439825	*Galerella pulverulenta*	Cape Grey mongoose
K5	22/06/2018	17:54	-33,651469	18,439825	*Caracal caracal*	Caracal
K5	27/06/2018	02:07	-33,651469	18,439825	*Genetta genetta*	Small-Spotted genet
K5	13/07/2018	02:32	-33,651469	18,439825	*Genetta genetta*	Small-Spotted genet
K5	14/07/2018	16:08	-33,651469	18,439825	*Galerella pulverulenta*	Cape Grey mongoose
K5	16/07/2018	23:57	-33,651469	18,439825	*Genetta genetta*	Small-Spotted genet
K7	08/06/2018	02:14	-33,619546	18,424991	*Caracal caracal*	Caracal
K10	05/12/2018	11:10	-33,635380	18,415699	*Galerella pulverulenta*	Cape Grey mongoose
K10	15/05/2018	19:19	-33,635380	18,415699	*Mellivora capensis*	Honey badger
K10	12/05/2018	11:10	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	15/06/2018	13:03	-33,634001	18,417965	*Mellivora capensis*	Honey badger
K11	08/07/2018	16:30	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	08/07/2018	17:20	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose

Site	Date	Time	Latitude	Longitude	*Species*	Common name
K11	15/05/2018	14:00	-33,634001	18,417965	*Mellivora capensis*	Honey badger
K11	31/05/2018	22:10	-33,634001	18,417965	*Genetta genetta*	Small-Spotted genet
K11	02/08/2018	01:20	-33,634001	18,417965	*Panthera pardus*	Leopard
K11	04/08/2018	12:00	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	07/08/2018	17:50	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	07/08/2018	09:10	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	12/08/2018	11:35	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	25/07/2018	12:58	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	27/07/2018	15:23	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	31/07/2018	16:04	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	31/07/2018	17:00	-33,634001	18,417965	*Mellivora capensis*	Honey badger
K11	01/08/2018	12:10	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	01/08/2018	12:40	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	14/04/2019	15:54	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K11	16/04/2019	10:43	-33,634001	18,417965	*Caracal caracal*	Caracal
K11	28/04/2019	11:10	-33,634001	18,417965	*Galerella pulverulenta*	Cape Grey mongoose
K13	27/07/2018	23:00	-33,633855	18,429280	*Genetta genetta*	Small-Spotted genet

Appendix 2: The presence of prey taxa in the diet of snake species that occur in Koeberg Nature Reserve from the literature

Prey type	*Crotaphopeltis hotamboeia*	*Dasypeltis scabra*	*Homoroselaps lacteus*	*Lycodonomorphus inornatus*	*Naja nivea*	*Psammophis crucifer*	*Psammophis leightoni*	*Psammophylax rhombeatus*	*Pseudaspis cana*
AMPHIBIA									
Anura									
Breviceps rosei	*x*	-	-	-	*x*	-	-	*x*	-
Strongylopus grayii	*x*	-	-	-	*x*	-	-	*x*	-
Tomopterna delalandii	*x*	-	-	-	*x*	-	-	*x*	-
MAMMALIA									
Rodentia									
Acomys subspinosus	*x*	-	-	*x*	*x*	-	-	*x*	*x*
Dendromus melanotis	*x*	-	-	*x*	*x*	-	-	*x*	*x*
Dendromus mesomelas	*x*	-	-	*x*	*x*	-	-	*x*	*x*
Desmodillus auricularis	*x*	-	-	*x*	*x*	-	-	*x*	*x*
Gerbilliscus afra	*x*	-	-	*x*	*x*	-	-	*x*	*x*
Gerbillurus paeba	*x*	-	-	*x*	*x*	-	-	*x*	*x*
Mus minutoides	*x*	-	-	*x*	*x*	-	-	*x*	*x*
Steatomys krebsii	*x*	-	-	*x*	*x*	-	-	*x*	*x*
Otomys irroratus	*x*	-	-	*x*	*x*	-	-	*x*	*x*
Rhabdomys pumilio	*x*	-	-	*x*	*x*	-	-	*x*	*x*
Eulipotyphla									
Myosorex varius	*x*	-	-	*x*	*x*	-	-	*x*	*x*
REPTILIA									
Scincidae									
Acontias meleagris	-	-	*x*	-	*x*	*x*	*x*	*x*	-
Scelotes bipes	-	-	*x*	-	*x*	*x*	*x*	*x*	-

Appendix 3: Continued

Prey type	Crotaphopeltis hotamboeia	Dasypeltis scabra	Homoroselaps lacteus	Lycodonomorphus inornatus	Naja nivea	Psammophis crucifer	Psammophis leightoni	Psammophylax rhombeatus	Pseudaspis cana
Trachylepis capensis	-	-	-	-	*x*	*x*	*x*	*x*	-
Trachylepis homalocephala	-	-	-	-	*x*	*x*	*x*	*x*	-
Trachylepis variegata	-	-	-	-	*x*	*x*	*x*	*x*	-
Gekkonidae									
Afrogecko porphyreus	*x*	-	-	-	*x*	*x*	*x*	*x*	-
Pachydactylus austeni	*x*	-	-	-	*x*	*x*	*x*	*x*	-
Pachydactylus geitje	*x*	-	-	-	*x*	*x*	*x*	*x*	-
Lacertidae									
Meroles knoxii	*x*	-	-	-	*x*	*x*	*x*	*x*	-
Gerrhosauridae									
Gerrhosaurus typicus	*x*	-	-	-	*x*	*x*	*x*	*x*	-
Typhlopidae									
Rhinotyphlops lalandei	-	-	-	-	*x*	*x*	*x*	-	-
Colubridae									
Crotaphopeltis hotamboeia	-	-	-	-	*x*	-	-	-	-
Dasypeltis scabra	-	-	-	-	*x*	-	-	-	-
Lamprophiidae									
Homoroselaps lacteus	-	-	-	-	*x*	*x*	*x*	-	-
Lycodonomorphus inornatus	-	-	-	-	*x*	-	-	-	-
Psammophis crucifer	-	-	-	-	*x*	*x*	*x*	-	-
Psammophis leightoni	-	-	-	-	*x*	*x*	*x*	-	-
Psammophylax rhombeatus	-	-	-	-	*x*	*x*	*x*	-	-
Pseudaspis cana	-	-	-	-	*x*	-	-	-	-