QUANTIFYING COMPETITION IN TWO CO-OCCURRING SOUTHERN AFRICAN PSAMMOPHIINAE SNAKES: *PSAMMOPHIS CRUCIFER* AND *PSAMMOPHYLAX R. RHOMBEATUS*

Silindokuhle Tokota

MSc degree

Supervisor: Dr. Bryan Maritz

Submitted in fulfilment of the requirements for the degree of Master of Science

Faculty of Natural Sciences

Department of Biodiversity and Conservation Biology
University of the Western Cape
Bellville, South Africa
November 2020

Declaration

I declare that "QUANTIFYING COMPETITION IN TWO CO-OCCURRING SOUTHERN AFRICAN PSAMMOPHIINAE SNAKES: *PSAMMOPHIS CRUCIFER* AND *PSAMMOPHYLAX R. RHOMBEATUS*" 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: Silindokuhle Tokota Date: December 2020

Signature: S Tokota

Acknowledgements

First and foremost, I would like to extend special thanks to my supervisor Dr. Bryan Maritz. The road to reaching this final product was full of bumps, hiccups, and surprises. You were extremely supportive both as my academic mentor and friend when this journey hit its lows, as well as when it hit its heights. You were my life jacket at times I seemed too spent to continue. Moreover, you taught me a lot of valuable skills that I will carry with me for the rest of my personal and professional life. You were my senzu bean.To you I say… Iyabulela ilali, enkosi grootman!

This one goes to Prof. Mark Gibbons and Linda van Heerden. You guys were everything to me…my friends, mentors, colleagues and sometimes parental figures. I appreciate everything you have done for me since I joined our department from undergrad, straight to the end of my MSc. To you I say…Nangamso!

Thank to Robin Maritz for providing me with the dietary data used in my analysis. To you I say…Udlalile sisteri

Jody Barends! I thank you for all the help you provided when it came to some of those sticky situations that wanted to become the enemy of progress in my mark-recapture analysis. To you I say… ungaza kum naninina for isonka esinecheese. Enkosi bhuti!

Lindiwe Makasi and Duimelize Kemp. You guys were my pillars of strength. Whenever I had negative thoughts about taking it easy and not pull through, I took one look at your guys and I would remember that I was doing it for our future as well. Thank you for believing in me, pushing me and supporting me through all my schooling years. I love you both and you shall reap the fruits of your efforts. To you I say…Nizimbokodo endinohlanganisa ngazo naphinah ebomini bam!

Special thanks to my constant field-partner Bryan Cloete. You have been extremely helpful in making sure I got to the field to sample, as well as being there all the way during the sampling. Also, I would like to thank Riaaz Mohamed and Tim Ponton for occasionally helping me in the field. All of you guys were Too Class and I look forward to any future collaborations we may have. To you guys I say…enkosi befethu, masiyifake ityiwa ingonakali

Last but not least, I want to thank Jurina Le Roux from the conservation department at the Koeberg Private Nature Reserve making sure we had a smooth experience working in the reserve. To you I say…sibamba ngazbini

ABSTRACT

Studies on snake competitive interactions have relatively been well documented globally, however, those examples tend to be dominated by non-African examples. Africa has a large and spectacular reptile diversity and yet robust and empirical studies on snake population ecology remain poorly understood or documented. Given the close phylogenetic relationship between the two species, as well as the remarkable similarities in overall appearance, morphology, reproductive biology, and most importantly geographic distribution, *Psammophis crucifer* and *Psammophylax rhombeatus* offered an ideal study system in which to ask questions related to interspecific competition and niche partitioning. Specifically I asked (1) whether broad scale geographic sympatry is facilitated by fine-scale allopatry through separation of space-use, and (2) whether the diets of the two species provided evidence of partitioning along the dietary niche. To answer these questions, I first quantified relative abundance of the two species at a fine scale, and secondly used existing dietary data to quantify dietary niche overlap. Even though *P. rhombeatus* was always more abundant in my sample, I found no evidence of space-use partitioning in this study, instead it showed a positive correlation in their abundance, and therefore suggesting space was not a limiting resource. Pianka niche overlap analysis showed significant differences in their feeding habits whereby *P. rhombeatus* had a broader diet which included mammals and birds, whereas *P. crucifer* predominantly fed on lizards and other snakes. In conclusion, my study suggests that across multiple geographic scales these two snakes use the same spatial resources and are able to co-exist by partitioning food resources. Lastly, my study serves to provoke more African studies of this nature with suitable candidate snake species.

Keywords: Competition, Niche partitioning, *Psammophylax r. rhombeatus*, *Psammophis crucifer*, abundance, scale, space, diet, co-existence

List of Figures

Figure 9: Proposed trapping design using ACO for estimating snake densities in future studies. White squares represent existing ACO layout; Black squares represent additional boards to be added.

Figure 10: Both species occupying the same ACO (top). Intra-guild predation, big *P. crucifer* eating a small *P. rhombeatus* (bottom). Photo cred: Hannelie Fourie Coetzee. Source: Facebook group Predation Records: Reptiles and Frogs (Sub-Saharan Africa).

List of Tables

Table of Contents

1. INTRODUCTION

The drive for individuals to acquire resources that are essential for their survival can result in competition if those resources are in limited supply (Park, 1962; Schoener, 1983; Begon *et al*., 2006). This competition is widely defined as the interaction brought about by sharing a resource in limited supply, and a reduction in fitness of at least one of the involved individuals (Park, 1962; Schoener, 1983; Begon *et al*., 2006). Reduction in fitness may occur as a result of two widely accepted types of competition—intraspecific and interspecific competition. The former is a result of competition between members of the same species, whereas the latter is competition between members of different species (Begon *et al*., 2006). Competition has been well documented in numerous taxa including plants (Tansley, 1917), crustaceans (Connell, 1961), diatoms (Tilman *et al.*, 1981), fish (Taniguchi and Nakano, 2000), birds (Martin and Martin, 2001) and many others, as an important driver of broad ecological community patterns. Competition is one of three ecological processes which usually operate together to produce the ecological patterns observed in the natural world (Toft, 1985). Other ecological processes include predation and/or other factors which are independent of intraspecific or interspecific interactions (e.g. physiological constraints) which may work in unison to bring about the existence of diverse ecological patterns (Toft, 1985).

The concept of a niche is a profound concept in ecology that aims to explain ecological biodiversity patterns in ecosystems (Shroener, 1974; Love, 1977; Costa-Pereira *et al.*, 2019). Niche refers to the position of an individual in its environment with respect to resource availability and accessibility (Love, 1977). A fundamental niche refers to the total suite of ecological conditions in which a species could potentially survive and reproduce (Love, 1977; Krebs, 1972). However, because of limiting ecological processes such as competition and physiological constraints, species tend to occupy a subset of a fundamental niche called the realized niche (Love, 1977; Krebs, 1972) See Fig. 7.7 in Krebs, 1972 for schematic illustration differentiating fundamental and realised niche for plant species, where temperature and soil moisture are the major limiting ecological processes). Furthermore, niche theory predicts that for ecologically-similar, sympatric species to coexist without competitive exclusion there has to be a degree of variation in their use of shared resources to promote co-existence (Park, 1962; Shroener, 1983; Begon *et al*., 2006). Studies that investigate niche partitioning do so by examining data relating to diet (food), space (spatial), and time (temporal) because they form the fundamental categories in which niche partitioning can take place (Love, 1977).

Darwin’s finches on the Galápagos Islands offer a good example of the above mentioned phenomena, whereby the birds were able to co-exist by eating different sized seeds, which corresponds with the morphological evolution of complementary beak sizes (Abzhanov *et al*., 2004). In this example, we see co-existence between similar species through dietary niche partitioning that is ultimately important in establishing the finches’ community structure on the islands. Similarly, niches can be partitioned by physically (spatially) occurring in slightly different parts of the same habitat or with different patterns of circadian rhythm (time) to minimize competition for those shared resources. For example, Luiselli *et al.* (2012) showed that two whip snake species in Sardinia demonstrate how ecologically similar species partition their habitats as well as how traits can shift in areas of localised distribution overlap where spatial partitioning does not occur. In this example, we see evidence of smaller body sizes for the weaker syntopic competitor (Luiselli *et al.*, 2012). It is also important to note that the intensity of competition can vary seasonally, depending on abundance and availability of a limiting resource. For example, during the wet season in Nigeria, there is an increase in prey biomass because of highly abundant rodents and amphibians, resulting in a reduction in competition intensity between local aquatic snakes (Akani *et al*., 2004; Angelic and Luiselli, 2005).

Competitive exclusion occurs when there is a lack of niche partitioning between sympatric competing species, resulting in the stronger opponent out-competing its relatively weaker competitor (Lotka, 1932; Gause 1934; MacArthur and Levins, 1967; Tilman, 1981). Although there has been a growing pool of literature regarding the mechanisms that drive the existence of such ecological patterns being observed in nature (Shroener, 1974; 1983; Janzen, 1976; Toft, 1985), there remain locations around the world where this knowledge is extremely poor. Knowledge of snake competitive interactions tends to be dominated by non-African examples. Apart from Africa, niche partitioning in snakes has been documented in other parts of the world including North America (Steen *et al.*, 2014; Perkins *et al.*, 2020), South America (Teixeira *et al.*, 2017; Pietro *et al.*, 2020), Australia (Goodyear and Pianka, 2008), Asia (Rahman, 2014) and Europe (Luiselli, 2006a). Africa on the other hand has a large and spectacular reptile diversity and yet robust and empirical studies on snake population ecology remain poorly understood or documented because of the challenges associated with studying herpetofauna (Janzen, 1976; Toft, 1985; Maritz, 2011; Maritz and Alexander, 2012; Tolley *et al*., 2016). This gap in the knowledge can be attributed to the lack of sampling, and organismal traits that results in low detectability of reptiles in general (Guisan *et al*., 2006; Bombi *et al*., 2009; Tolley *et al*., 2016).

The existing studies on competition in African snake communities took place in the tropical forests of Nigeria, where snake communities can consist of up to 24 different snake species (Andreone and Luiselli, 2000). To date, there are two studies that demonstrate evidence of habitat partitioning in which the snakes were found to co-exist by slightly varying their locations between terrestrial, arboreal, aquatic, or subterranean microhabitats (Luiselli and Akani, 1999; Luiselli and Angelici, 2000). Four studies demonstrate partitioning through diet differentiation where congeneric species had relatively high dietary overlap, but niche partitioning took place in the context of consuming different size classes of the same prey types (Luiselli *et al*., 1998; Luiselli and Akani, 2003; Luiselli, 2003; Luiselli, 2006b).

The family Psammophiidae includes seven genera and 53 extant species of snakes, with geographic distributions that spread throughout Africa, Madagascar, and into Europe and Asia (Broadley, 1977; Branch 1998; Broadley, 2002; De Haan, 2003; Kelly *et al*., 2008; Branch *et al*., 2019). Seven of these species belong to the genus *Psammophylax* and 34 belong to the genus *Psammophis* (Branch, 2019; Keates *et al*., 2019). The most recent taxonomic review of the family Psammophiidae shows that the two aforementioned genera are sister taxa (Vidal *et al*., 2008; Branch *et al*. 2019).

In this thesis, I focus on two similar southern African snakes, the Spotted skaapsteker (*Psammophylax rhombeatus*) and Cross-marked grass snake (*Psammophis crucifer*; Fig. 1). These two species both have cylindrical slender bodies with long thin tails, covered in smooth dorsal scales (Branch, 1998; Shine *et al*., 2006; Alexander and Marais, 2007). They have moderate to relatively large eyes, with round pupils that may be advantageous to their diurnally active behaviour (Alexander and Marais, 2007; Branch, 1998). In this paragraph the following comparisons are in order of *P. rhombeatus* (former), followed by *P. crucifer* (latter). They have a closely related number of mid-body row scales, 17 and 15, respectively (Branch, 1998; Alexander and Marais, 2007). They have a divided anal shield and overlap in the number of ventral scales, 139 – 177 vs 134 – 201, as well as in the paired number of sub-caudal scales 49 – 84 vs 61–156, respectively (Branch, 1998; Alexander and Marais, 2007).

Figure 1: Study species (A) Spotted skaapsteker (*Psammophylax rhombeatus*) and (B) Cross-marked grass snake (*Psammophis crucifer*) from Koeberg Nature Reserve, WC. Photo credit: Bryan Maritz.

Both species show sexual size dimorphism with males being larger than females in *P. rhombeatus* and females being larger than males in *P. crucifer* (Cottone and Bauer, 2010). Because adult *P. crucifer* are slightly smaller than adult *P. rhombeatus*, they have slightly smaller clutch sizes, with a maximum of 13 eggs (18 – 21 mm x 10 mm) and 30 eggs (20 – 35 mm x 12 – 18 mm), respectively (Branch, 1998). Their diets predominantly include varying proportions of small vertebrates inclusive of frogs, lizards, small mammals, and even other snakes (Branch, 1998; Alexander and Marais, 2007). Both species are mildly-venomous and inject venom through rear immovable fangs situated on the maxillary bone, below the eyes (Alexander and Marais, 2007). When disturbed, they typically quickly slither through bushes/grasses and further aid their escape by suddenly remaining motionless until it is safe or safer to move on (Alexander and Marais, 2007). Finally, both species are endemic to southern Africa, share similar geographic distributions, and are widespread and common where they occur (Branch, 1998; Alexander and Marais, 2007; Bates *et al.,* 2014; Cottone and Bauer, 2010; Fig. 2).

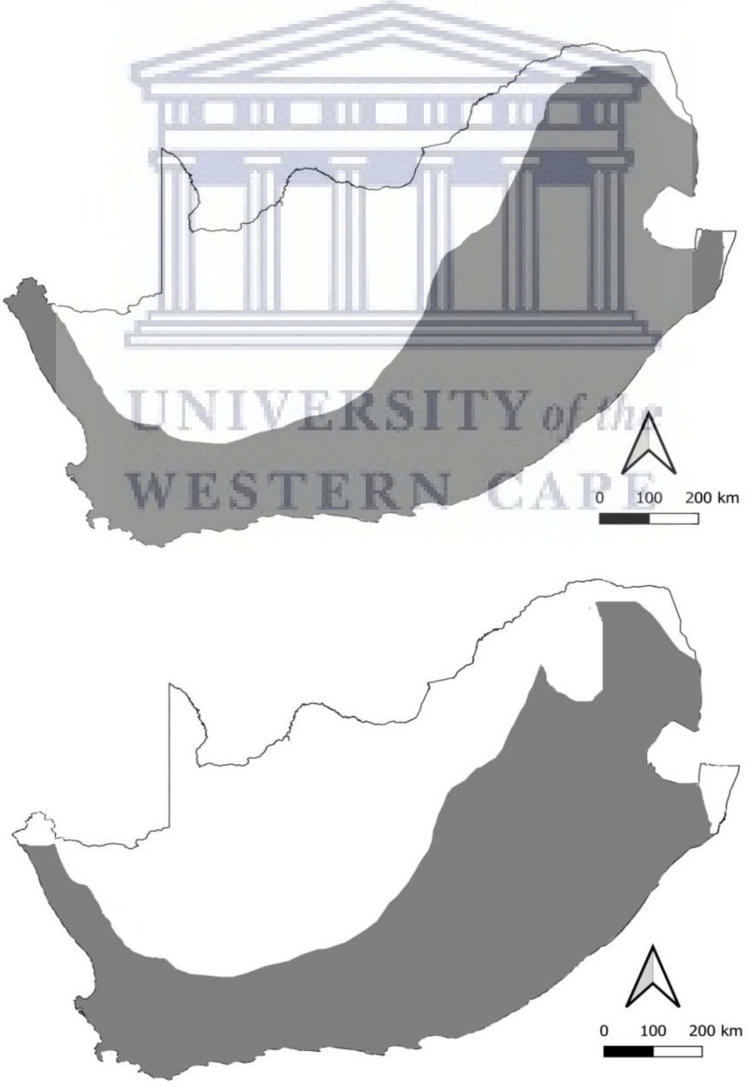

Figure 2: Geographic distributions of (A) *Psammophylax rhombeatus* and (B) *Psammophis crucifer* in South Africa.

Given the close phylogenetic relationship between the two species, as well as the remarkable similarities in overall appearance, morphology, reproductive biology, and most importantly geographic distribution, *Psammophis crucifer* and *Psammophylax rhombeatus* offer an ideal study system in which to ask questions related to interspecific competition and niche partitioning. Specifically I asked (1) whether broad scale geographic sympatry is facilitated by fine-scale allopatry through separation of space-use (hereafter referred to as ***spatial partitioning***), and (2) whether the diets of the two species provided evidence of partitioning along the dietary niche axis (hereafter referred to as ***dietary partitioning***).

I aimed to investigate interspecific competition in two similar southern African snakes, *Psammophylax rhombeatus* and *Psammophis crucifer* through two objectives. These were to (1) quantify relative abundance of the two species at a fine scale, and (2) use existing dietary data to quantify dietary niche overlap.

2. METHODS

2.1. Spatial partitioning

2.1.1. Study site

The Koeberg Private Nature Reserve (KNR) is situated in the Western Cape Province of South Africa, where it forms part of the Cape Floristic Region biodiversity hotspot (Linder *et al*., 2010; Fig. 3). The region has a Mediterranean climate, characterized by winter rainfall (Linder, 2003). Koeberg Private Nature Reserve is located on the west coast of the Western Cape, approximately 35 km north of the city of Cape Town. The area has an average daily maximum temperature of 17 °C and 28 °C in winter and summer respectively (Le Roux, 2014). It receives an average of 372 mm of rainfall annually, however, the two years preceding my study had produced record low rainfalls (Koeberg Private Nature Reserve, Unpublished data). Vegetation in the area is dominated by Atlantis Sand Fynbos and Cape

Flats Dune Strandveld (Mucina and Rutherford, 2006). *Psammophis crucifer* and *Psammophylax rhombeatus* are both abundant at KNR where they occur sympatrically with another psammophiid, *Psammophis leightoni*, and several other snake species including: *Crotaphopeltis hotamboeia*, *Dasypeltis scabra*, *Dispholidus typus*, *Homoroselaps lacteus*, *Lycodonomorphus inornatus*, *Naja nivea*, *Pseudaspis cana*, and *Rhinotyphlops lalandii* (Maritz lab, Unpublished data).

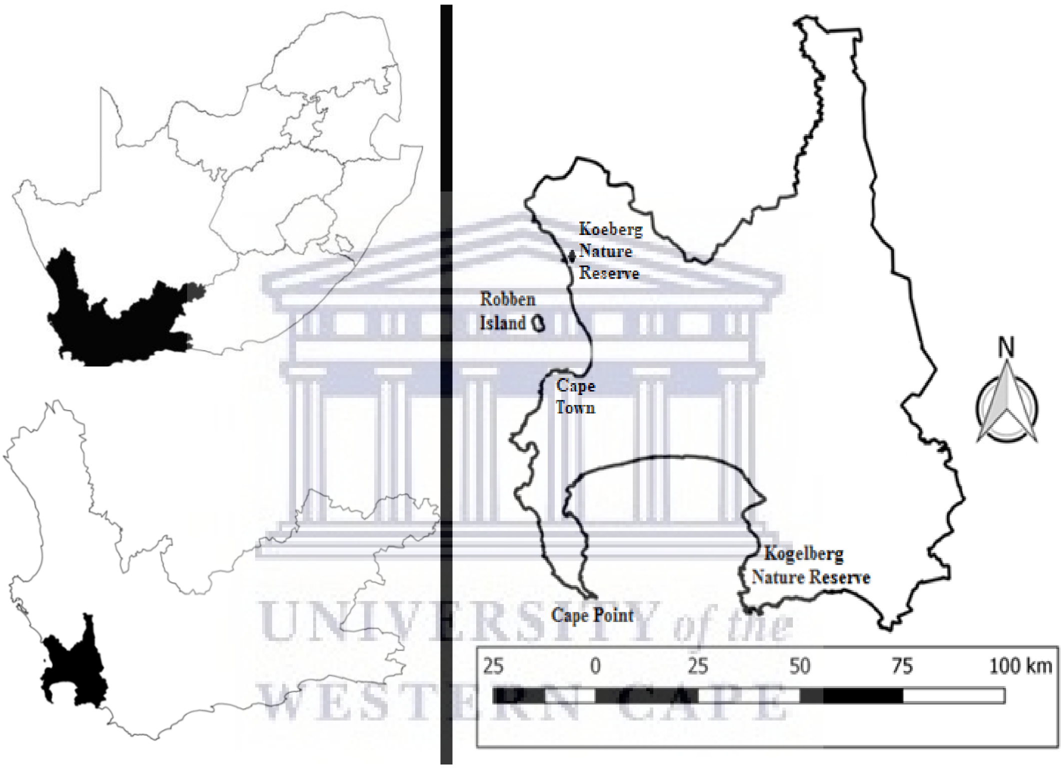

Figure 3: Map of South Africa (top left) highlighting the Western Cape Province, and the Cape Town Metropolitan area within the province (bottom left). My study took place at Koeberg Private Nature Reserve in the north-western corner of the Cape Town Metropolitan Area (right).

2.1.2. Sample site selection

Ten sites were selected at the Koeberg Private Nature Reserve, Western Cape, South Africa to study patterns of co-occurrence between *Psammophis crucifer* and *Psammophylax rhombeatus*. The numbering of the different sites was arbitrary and does not necessarily reflect or follow a chronological order. The reserve management had cleared some parts of the reserve of alien *Acacia* vegetation, as part of their alien vegetation management. Additionally, the reserve experienced a wild fire that burnt though parts of the reserve in 2016. As a result, my focal sites were stratified across three vegetation units: three ‘burnt’ sites for the areas that burned in 2016, three ‘cleared’ for the areas cleared of alien invasive vegetation, and finally four ‘natural’ sites for everything else that was not cleared or burnt. Sites were between 250 m and 5.5 km from each other. Despite marking over 150 individual snakes (multiple species), no snake was ever recaptured at a different site to that at which it was initially captured, suggesting that my sites were likely to be independent of each other.

2.1.3. Snake sampling methods

Each site covered an area of approximately 1 ha. I placed twenty-five wooden (600 mm x 600 mm x 18 mm) artificial cover objects (ACOs) approximately 25 m apart in a grid-like format (Fig. 4) and surveyed them twice a month for the presence of snakes over a period of 33 months (2016 – 2018). Surveys during 2016 and 2017 were largely *ad hoc*, but I undertook detailed surveys in 2018. Note that these surveys were initiated as early as my undergraduate studies where I was involved in the study as a volunteer, and carried through to the last year of sampling during which I surveyed each site twice a week.

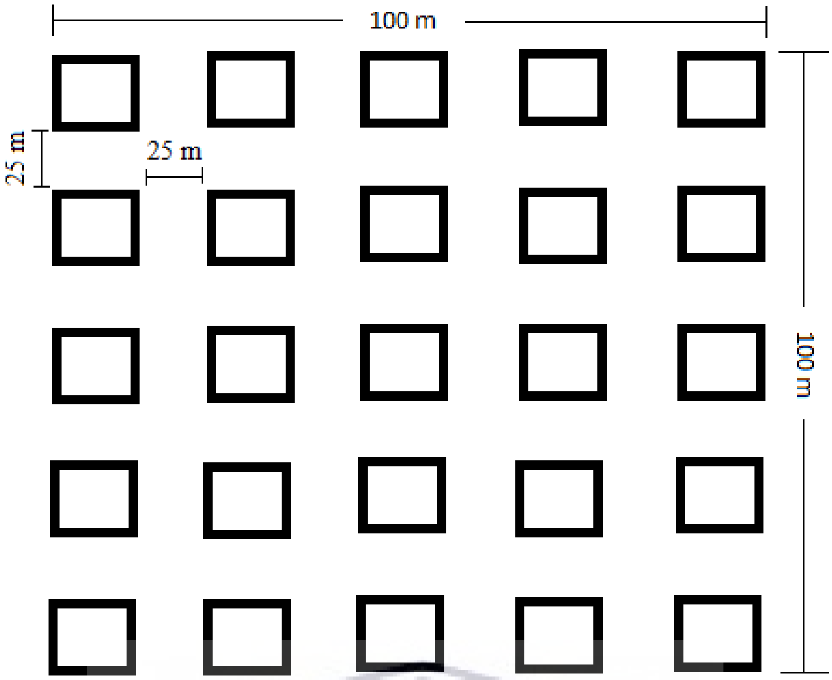

Figure 4: Schematic diagram (aerial view) of the ACOs placed out at each of the ten sites in the study area.

All captured snakes were uniquely marked via ventral scale clipping (Plummer and Ferner, 2012) and measured for snout-vent length, tail length, and mass as part of a separate study. All captured animals were released immediately after processing at their exact sites of capture.

2.1.4. Statistical analyses

My objective for this section of the thesis was to compare the abundances of *Psammophis crucifer* and *Psammophylax rhombeatus* across the 10 sample sites to examine the degree to which their abundances were correlated. I used four different methods to estimate abundance: raw counts, Cormack-Jolly-Seber mark-recapture (CJS) analysis, Royle-Nichols occupancy (RN) analysis, and spatially-explicit capture recapture (SECR) analysis. I hypothesised that if spatial niche partitioning was taking place I would detect a negative relationship between the abundance measures of the two species. Conversely, if abundances showed a positive relationship or no relationship, then I would interpret those findings as a lack of evidence for spatial niche separation.

2.1.4.1. Raw count data

I summarised raw capture rates of each species at each site. I compared site-specific counts of the total number of unique animals for each species at each site using linear regression to test the null hypothesis that there was no relationship between the raw count abundance of each species across the sites. I additionally compared raw capture rates for the two species by conducting a paired t-test, to test the hypothesis that the two species are detected at similar frequencies across the study sites.

2.1.4.2 Cormack-Jolly-Seber mark recapture

In an attempt to gain more robust insights into the abundances of the two species across the sites while accounting for imperfect detection, I used the Cormack-Jolly-Seber (CJS) estimation model. This model uses a regression parameterization that allows individual, time, and individual-time varying covariates (Amstrup *et al*., 2010). I planned to use these models to estimate sites-specific abundance estimates for each species. I used all years capture history data to produce open population CJS time-dependent models with covariates for *Psammophis crucifer* and *Psammophylax rhombeatus* for each of the ten sites. The capture histories describe the encounter history of an individual for each sampling event, where ‘1’ means an individual was detected and where ‘0’ means it was not detected (Amstrup *et al*., 2010). The models were produced using an explicit 2-D matrix method, which allows the construction of a specific 2-D matrix for selected covariates. I constructed a standard 2-D matrix using season as a covariate for all parameters, where ‘1’ represented the rain and ‘0’ represented the dry season for all sampling years in monthly intervals. The rainy (Apr – Aug) and dry (Sep – Mar) seasons were derived from the associated pattern of high capture probabilities coinciding with the rainy season from my field data.

I fit four different models in which (i) capture and survival probabilities were kept constant through time [$\varphi(.)p(.)$], (ii) survival probability was kept constant and capture probability varied with season [φ(.)p(season)], (iii) capture probability was kept constant and seasonal survival probability varied [φ(season)p(.)], and (iv) survival and capture probabilities varied with season [φ(season)p(season)]. Because the number of *P. crucifer* caught were always less than that of *P. rhombeatus*, I additionally included the count data for *P. crucifer* as a covariate through allthe *P. rhombeatus* models. These models were produced using the CJS function 'F.cjs.estim' from an R package called 'mra' on R, version R 3.5.3 (R core team 2020). Model outputs included population size estimates, apparent survival, and capture probability for each species across all sites. The best performing model was selected based on the model with the smallest sample adjustment AIC_c (e.g. Akaike 1973, Burnham and Anderson, 1998), where the model with the lowest AIC_c was considered to be the best performing model (Royle and Nichols, 2003).

2.1.4.3 Occupancy modelling approach

I used the Royle-Nichols approach (Royle and Nichols, 2003) to produce a 'single-season occupancy' model for each site, per species. However, instead of using the entire data set collected since 2016, I reduced the sampling data to only six sampling events that took place in the winter of 2018 in order to maximize captures and fit the 'single-season occupancy' model. It is important to note that in this model the absence-presence is also denoted by '0' and '1', however, in this case a '0' means the species was not detected, whereas '1' means the species was detected in that sampling event at that site (Royle and Nichols, 2003). In this type of model, non-detections can be ambiguous in the sense that an species can be present at a site, but not detected, or the species may not be occupying the site at all in which case you will still record it as '0' (Royle and Nichols, 2003). I used an R package 'wiqid' on R, version R 3.5.3 where the function 'occSSrn' allows for site-specific covariates to be included in the 'single-season occupancy' model. The standard basic model [lambda(.) r(.)] was allowed to vary with respect to the covariates that were included in building each of the unique model types, per species. Covariates included in these models had one or two of the following covariates fitted into the model (1) 'site' (unique site), (2) 'competitor' (number of co-occurring *P. rhombeatus* or *P. crucifer* at a site), and (3) 'veg' (site category: burnt; cleared; and natural), see Table 2. Similarly to the Cormack-Jolly-Seber model outputs, the best performing model was selected on the basis of having the lowest AIC score. The best performing model was finally used to estimate the site-specific abundance for each species. I compared site-specific estimates of N from the best fit Royle-Nichols model for the two species using linear regression.

2.1.4.4 Spatially-explicit Capture Recapture

In addition, I estimated snake densities in a spatially-explicit framework. I used the SECR package (Efford, 2015) in R 3.5.3 (R core team 2020) to estimate snake densities for *Psammophylax rhombeatus* and *Psammophis crucifer* across each of the 10 sites. Because the ACOs that were used allowed more than one individual to be trapped at any time, I used the "multi" detector function to build the models (Efford, 2015). Moreover, I used the half-normal detection function and a 100 m habitat mask buffer around the artificial cover objects for each site. Lastly, the overall model was standard because all 'real' parameters which included density (D), detection parameters (g0), and sigma, were kept constant (i.e. D~1, g0~1, sigma~1; Efford, 2015). Lastly, I used the estimates to plot a regression and perform a linear regression analysis.

2.2. Dietary partitioning

2.2.1. Sources of information

I searched the literature for all the existing published dietary records of *P. crucifer* and *P. rhombeatus* (see Table 3 for sources). The data sources came from peer-reviewed journals as well as grey literature. Upon request, I received citizen science diet data for both species from the publishing authors of Maritz and Maritz (2020), who are the co-founders of the social media page called Predation Records - Reptiles and Frogs group on Facebook (https://www.facebook.com/groups/888525291183325). This Facebook platform is a unique online database that formally reports the natural history of reptiles and amphibians, primarily relying on the submission of observation dates, species identity, pictures, and videos observed by citizens as evidence of predation events (Maritz and Maritz, 2020). Details about how the citizen science dataset was collected and maintained are thoroughly outlined in the recently published work by Maritz and Maritz (2020).

2.2.2. Statistical analyses

I pooled and summarised all dietary records for each species for analysis. The prey items were grouped into the lowest taxonomic level that was inclusive of all representatives of that prey type. I chose a total of six types of prey groups which included the following groups names: snakes, lizards, birds, mammals (inclusive of all small rodents and shrews), frogs, and arthropods. I used the number of prey records to calculate the proportion of each prey type in the diet of each species of predator. I used the resultant proportions in the Pianka niche overlap equation (below) to quantify dietary overlap between *P. crucifer* and *P. rhombeatus*.

$$O_{jk} = \frac{\sum_i^n P_{ij} \times P_{ik}}{\sqrt{\sum_i^n P^2{}_{ij} \times \sum_i^n P^2{}_{ik}}}$$

The Pianka niche overlap index (O_{jk}) measures the food resource (i) use overlap between species j and k, where P is the proportion of a food resource in the diet of species j and k. Finally, n reflects the total number of food resources. The value produced by this measurement may fall anywhere between 0 and 1, with low overlap resulting in values closer to 0 and higher overlap resulting in values closer to 1 (Pianka, 1974). The Pianka dietary niche overlap was calculated using the package EcoSimR in R 3.5.3 (Gotelli and Entsminger, 2006; R core team 2020). Because the interpretation of the measured Pianka value may be controversial with respect to whether the overlap is high or low, Da Silva *et al*., (2017) modified work by Grossman (1986) and Corrêa *et al*. (2011) and proposed a criterion that was followed in this study. According to this criterion, there are three classifications starting with low (0 – 0.39), followed by intermediate (0.4 – 0.6), and finally high (0.6 – 1) (Da Silver *et al*., 2017).

3. RESULTS

3.1. Spatial partitioning

3.1.1. Raw count data

The total number of unique snakes caught overall for all years summed up was 38 and 58 for *P. crucifer* and *P. rhombeatus*, respectively. A paired t-test between the number of unique *P. crucifer* and *P. rhombeatus* across all sites showed that the latter species was significantly ($t_9 = -2.24$; $p = 0.05$) captured more (mean ± SD = 5.8 ± 3.9 individuals.ha^{-1}) than the former (mean ± SD = 3.8 ± 3.1 individuals.ha^{-1}). Regression analysis additionally showed a significant positive relationship between the number of unique *P. rhombeatus* and *P. crucifer* across all ten sites (regression analysis, $F_{(9)} = 7.53$; $p = 0.03$; Pearson’s correlation $r = 0.70$; Fig. 5).

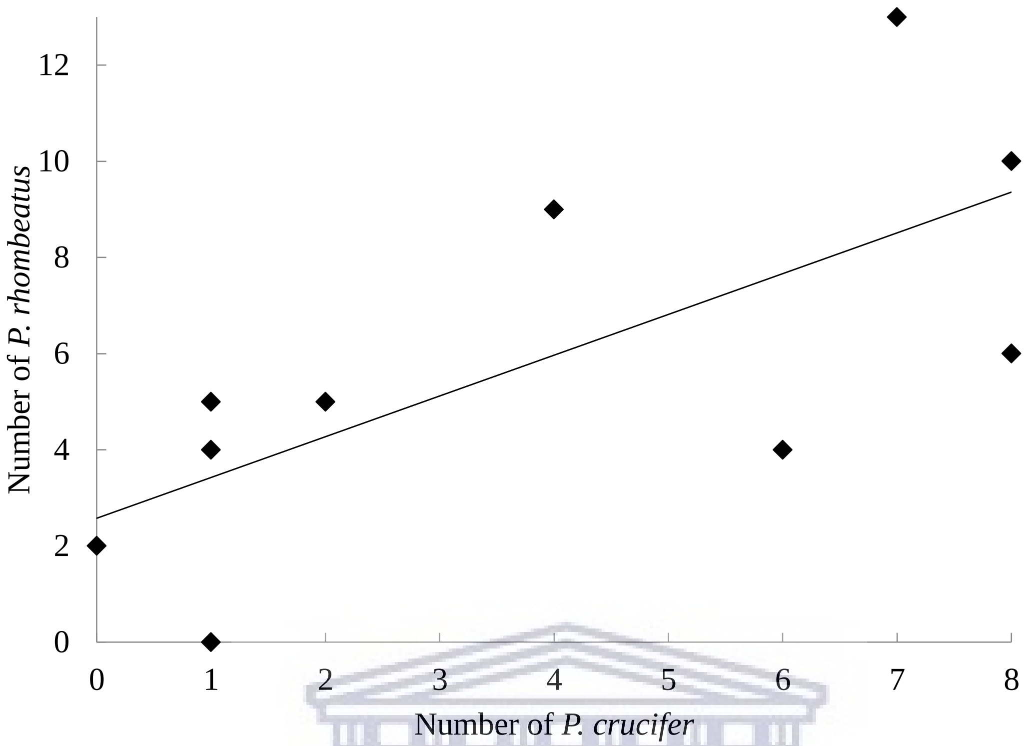

Figure 5: Linear regression between the number of unique of *P. rhombeatus* and *P. crucifer* recorded from each of 10 sample plots at Koeberg Private Nature Reserve between 2016 and 2018.

3.1.2. Cormack-Jolly-Seber mark recapture

I could not successfully estimate CJS parameters for either species across all sites (Table 1). The best performing models (where available) alternated between two similarly performing models ‘φ(.)p(.)’ and ‘φ(.)p(season)’. The number of parameters used in each model type is reported alongside each model type, and remained constant for each model type. Because *P. rhombeatus* had more captures and recaptures relative to *P. crucifer*, the majority of successful models were for the former species. For each species the model produced an estimated population size ($\hat{n}$) and standard error (SE) for each sampling event. I averaged the estimates from each sampling event for each species and site to produce the site-specific and species-specific estimates shown in Table 1. The sparser the data was for either species, the poorer the models performed due to model convergence failure. Failure of model convergence was most prominent in sites 10, 11, 12, and 13 for both species.

Table 1: Summaries for Cormack-Jolly-Seber model performance in estimating abundances for *P. crucifer* and *P. rhombeatus* where apparent survival is (φ), capture probability is (p), and average population size is ($\hat{n}$). Unsuccessful estimates demarcated with '--'.

			P. rhombeatus		*P. crucifer*	
Site	Model	# Par	AIC_c	$\hat{n}$ (SE)	AIC_c	$\hat{n}$ (SE)
1	φ(.)p(.)	2	31.93	--	32.15	3.83 (8.09)
	φ(.)p(season)	3	31.28	--	37.43	--
	φ(season)p(.)	3	29.08	0.64 (0.93)	36.91	--
	φ(season)p(season)	4	38.48	--	44.14	--
2	φ(.)p(.)	2	80.68	--	--	--
	φ(.)p(season)	3	80.21	2.14 (2.48)	--	--
	φ(season)p(.)	3	83.38	--	--	--
	φ(season)p(season)	4	83.19	--	--	--
5	φ(.)p(.)	2	34.78	0.69 (1.74)	32.15	3.32 (8.09)
	φ(.)p(season)	3	37.30	--	37.43	--
	φ(season)p(.)	3	41.56	--	36.91	--
	φ(season)p(season)	4	42.87	--	44.14	--
6	φ(.)p(.)	2	32.24	0.55 (1.07)	--	--
	φ(.)p(season)	3	51.97	--	--	--
	φ(season)p(.)	3	49.37	--	--	--
	φ(season)p(season)	4	--	--	--	--
7	φ(.)p(.)	2	39.95	--	46.33	--
	φ(.)p(season	3	--	--	--	--
	φ(season)p(.)	3	--	--	--	--
	φ(season)p(season)	4	-11.68	0.95 (1.94)	-3.07	1.22 (40.37)
8	φ(.)p(.)	2	23.72	1.71 (3.58)	18.05	--
	φ(.)p(season	3	32.80	--	10.50	5.18 (9.93)
	φ(season)p(.)	3	36.43	--	21.30	--
	φ(season)p(season)	4	61.98	--	13.60	--
10	φ(.)p(.)	2	50.19	--	--	--
	φ(.)p(season)	3	--	--	--	--
	φ(season)p(.)	3	--	--	--	--
	φ(season)p(season)	4	1.13	1.17 (2.40)	--	--
11	φ(.)p(.)	2	--	--	--	--
	φ(.)p(season)	3	--	--	--	--
	φ(season)p(.)	3	--	--	--	--
	φ(season)p(season)	4	--	--	--	--
12	φ(.)p(.)	2	--	--	--	--
	φ(.)p(season)	3	--	--	--	--
	φ(season)p(.)	3	--	--	--	--
	φ(season)p(season)	4	--	--	--	--
13	φ(.)p(.)	2	--	--	--	--
	φ(.)p(season)	3	--	--	--	--
	φ(season)p(.)	3	--	--	--	--
	φ(season)p(season)	4	--	--	--	--

3.1.3. Royle-Nichols occupancy model

Similarly to the CJS models, the best fitting model was selected based on having the lowest AIC score (Table 2). The best performing model was the basic ‘lambda(.) r(.)’ with no added covariates. However, the model ‘lambda (competitor) r(.)’ produced similarly low AIC scores to the best model (ΔAIC = 0.3 and 1.0 for *P. rhombeatus* and *P. crucifer* respectively). The finding that a model that includes competitor abundance produces comparable AIC scores circumstantially supports the finding that the abundances of the two species positively co-vary across the sites. The worst performing models all have ‘site’ as a covariate for both species, however, model ‘lambda(site + competitor) r(.)’ had the worst output, particularly for *P. crucifer* where no AIC score was produced at all (Table 2).

Table 2: Summary of Royle-Nichols models for the single-season occupancy estimation for *P. crucifer* and *P. rhombeatus*.

	P. rhombeatus		*P. crucifer*	
Model	# parameters	AIC	# parameters	AIC
lambda(.) r(.)	2	70.67	3	55.80
lambda(site) r(.)	9	81.62	4	68.19
lambda(competitor) r(.)	3	70.97	4	56.80
lambda(veg) r(.)	4	73.72	4	59.16
lambda(veg + competitor) r(.)	5	74.95	5	60.57
lambda(site + competitor) r(.)	10	83.62	5	--

I selected the best performing model ‘lambda(.) r(.)’ and used it to estimate the site-specific abundance for each species. Because two of the ten sites had extremely few captures, I was only able to estimate abundance for 8 sites. A linear regression analysis performed between the estimated abundance of *P. rhombeatus* and *P. crucifer* showed a positive relationship ($F_{(7)} = 11.71$; $p = 0.01$; Pearson’s correlation $r = 0.66$; Fig. 6). Moreover, to verify that the RN model estimates corresponded to the raw count data, I performed an additional linear regression between the raw capture data and the estimated abundance for each species. Those results revealed congruence between the raw count data and the modelled

RN estimates for both *P. crucifer* (t_7 = -8.78; r = 0.48; p <0.001) and *P. rhombeatus* (t_7 = -7.36; r = -0.17; p < 0.001).

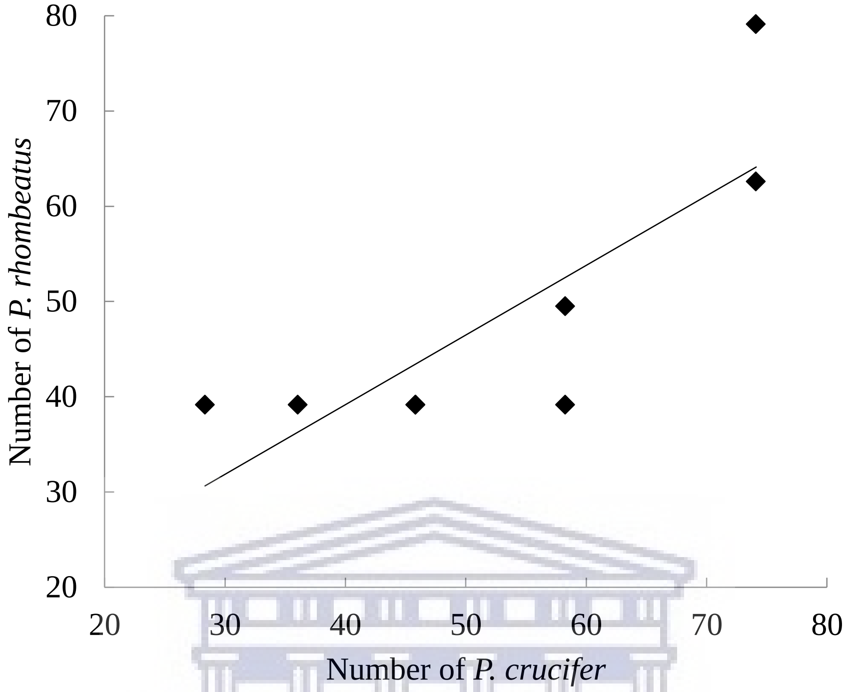

Figure 6: Linear regression between the Royle-Nichols estimated abundance from the occupancy modelling analysis of *P. rhombeatus* and *P. crucifer*. At least two of the eight sites shared abundance estimates.

3.1.4 Spatially explicit capture recapture

I was unable to estimate parameters for some of the sites for both species. *Psammophylax rhombeatus* had the most number of successfully estimated parameters compared to *P. crucifer*. Although not significant (p = 0.14) and despite the quality of the estimates produced by the SECR models, a regression analysis using these abundance estimates additionally showed a positive correlation between the estimated abundances of *P. rhombeatus* and *P. crucifer* across the four sites that produced estimates (regression analysis, $F_{(3)}$ = 19.37; p = 0.14; Pearson's correlation r = 0.95; Fig. 7). Even though the sample size reduces the inferential power of the analysis, the qualitative pattern is similar to that I found with the occupancy estimates as well as the number of unique individuals reported earlier.

Table 3: Shows the resultant snake density estimates from SECR models. Density = number of animals per hectare. Density CoV (Coefficient of variation) = Standard error of density estimate. g0 = probability of capture at home range centre. Sigma = spatial scale parameter (in meters). N = abundance at site (including buffer area). Because SECR added a 100 m buffer around each of the 1 hectare sites, the estimates (N) here are for an area of 9 hectares.

Site	Species	Density (95% CI)	Density CoV	g0 (95% CI)	Sigma (95% CI)	N (95% CI)
1	*P. rhombeatus*	1.912 (0.888 - 4.112)	0.407	0.003 (0.001 - 0.011)	75.616 (37.028 - 154.418)	18 (13 - 41)
1	*P. crucifer*	--	--	--	--	--
2	*P. rhombeatus*	3.836 (1.757 - 8.364)	0.415	0.006 (0.003 - 0.012)	47.169 (27.227 - 81.715)	36 (22 - 83)
2	*P. crucifer*	--	--	--	--	--
5	*P. rhombeatus*	2.641 (0.981 - 7.122)	0.541	0.002 (0.001 - 0.009)	65.568 (24.140 - 178.097)	17 (11 - 54)
5	*P. crucifer*	6.632 (4.014 - 68.916)	0.832	0.002 (0.001 - 0.012)	23.522 (8.612 - 64.237)	59 (26 - 160)
6	*P. rhombeatus*	0.909 (0.356 - 2.324)	0.508	0.001 (0.001 - 0.009)	54.013 (38.115 - 169.304)	9 (3 - 22)
6	*P. crucifer*	1.016 (0.3279 - 3.145)	0.628	0.004 (0.001 - 0.018)	69.868 (22.157 - 220.317)	9 (3 - 30)
7	*P. rhombeatus*	1.543 (0.661 - 3.600)	0.453	0.001 (0.001 - 0.003)	42. 364 (32.344 - 144.423)	10 (4 - 24)
7	*P. crucifer*	5.493 (1.432 - 21.058)	0.775	0.005 (0.002 - 0.016)	25.427 (10.460 - 61.811)	35 (9 - 135)
8	*P. rhombeatus*	4.138 (0.386 - 44.407)	0.826	0.002 (0.001 - 0.011)	45.199 (7.445 - 274.403)	32 (10 - 71)
8	*P. crucifer*	14.031 (3.233 - 60.884)	0.867	0.011 (0.002 - 0.061)	19.445 (13.934 - 32.674)	106 (24 - 464)
10	*P. rhombeatus*	5.654 (2.146 - 14.892)	0.526	0.019 (0.007 - 0.051)	12.804 (8.041 - 20.387)	34 (13 - 92)
10	*P. crucifer*	--	--	--	--	--
11	*P. rhombeatus*	12.146 (7.237 - 67.768)	0.620	0.021 (0.006 - 0.076)	16.616 (13.272 - 23.377)	125 (41 - 384)
11	*P. crucifer*	--	--	--	--	--
12	*P. rhombeatus*	--	--	--	--	--
12	*P. crucifer*	--	--	--	--	--
13	*P. rhombeatus*	--	--	--	--	--
13	*P. crucifer*	--	--	--	--	--

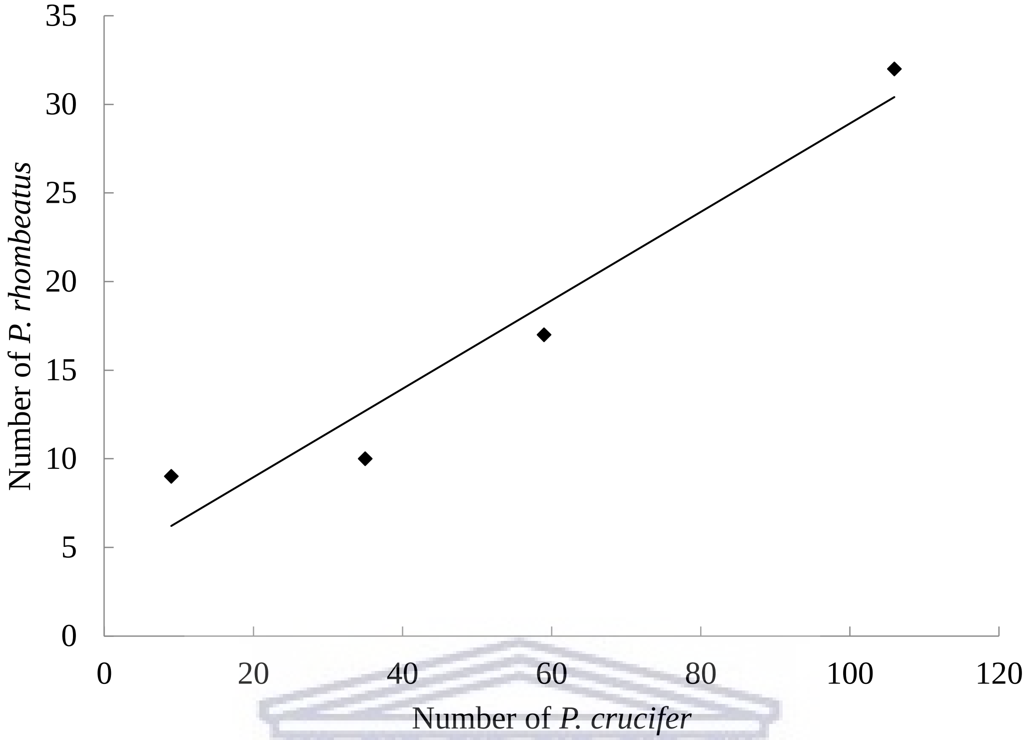

Figure 7: Linear regression for the estimated abundances of *P. rhombeatus* and *P. crucifer* using SECR models. These points represent only the four sites that I was able to successfully produce estimates.

3.2 Dietary partitioning

A search of the literature and social media produced a total of 184 dietary records for *Psammophis crucifer* and *Psammophylax rhombeatus*; 58 and 128 respectively (Table 3). The literature contributed most of the records as well as the oldest records, with observations dating back to the late 1800s. Conversely, the newly established social media data produced the fewest number of records (Table 3). The different types of prey were either shared by both snake species or were exclusively exploited by one species. The shared prey types varied in their relative consumption by either species. In proportion of the number of records, *P. crucifer* and *P. rhombeatus* fed minimally on arthropods, where arthropods only made up ~5 % of their diets combined (Fig. 8). Up to 23% of *P. rhombeatus* diet consisted of frogs, whereas frogs only made up ~7% of *P. crucifer* diet. The diet of *P. crucifer* consisted of about 79 % lizards, whereas lizards only made up ~16 % *P. rhombeatus* diet. Snakes were only found in the diet of *P. crucifer* (where they accounted for ~13 % of all observations). Lastly, *P. rhombeatus* additionally fed on birds (1 %) and somewhat extensively on mammals (57 %).

Of the six prey available prey categories *Psammophylax rhombeatus* consumed a wider range than *Psammophis crucifer*; 5 and 4 respectively. This finding suggests a wider diet for the former species (Fig. 9). *Psammophylax rhombeatus* was the only species to feed on mammals (57 %) and birds (1 %), whereas *P. crucifer* was the only species to feed on snakes (13 %; Fig. 9). However, in order of *P. rhombeatus* to *P. crucifer* respectively, the percentage proportion consumed were arthropods (3 %; 2 %), lizards (16 %; 79 %), and frogs (23 %; 7 %) were consumed by both species (Fig. 9). The Pianka niche index measured the level of dietary niche overlap and produced a very low dietary overlap of 0.28 between *P. crucifer* and *P. rhombeatus*.

Table 3: Summary of diet records for *Psammophylax rhombeatus* and *Psammophis crucifer* from the literature and citizen science.

	P. rhombeatus			*P. crucifer*		
Prey	No. of records	Proportion (%)	Sources	No. of records	Proportion (%)	Sources
Reptiles						
(Snakes)	0	0	--	7	12.5	Schönland, 1895; Cottone and Bauer 2010; citizen science.
(Lizards)	20	15.6	Cottone and Bauer, 2010; citizen science.	44	78.6	Fitzsimons, 1935; Fitzsimons, 1962; Broadley, 1966; De Waal, 1977; Branch and Braack, 1987; Van Wyk, 1988; Haagner and Branch, 1993; Branch and Bauer, 1995; Cottone and Bauer, 2010; citizen science.
Birds	1	0.8	Citizen science.	0	0	--
Mammals	73	57.0	Fitzsimons, 1962; De Waal, 1977; Van Wyk, 1988; Cottone and Bauer, 2010; citizen science.	0	0	--
Frogs	30	23.4	Fitzsimons, 1962; De Waal, 1977; Broadley, 1977; Douglas, 1990; Cottone and Bauer, 2008; Cottone and Bauer, 2010; citizen science.	4	7.1	De Waal, 1977; citizen science.
Arthropods	4	3.1	Cottone and Bauer, 2010.	1	1.8	Cottone and Bauer, 2010.

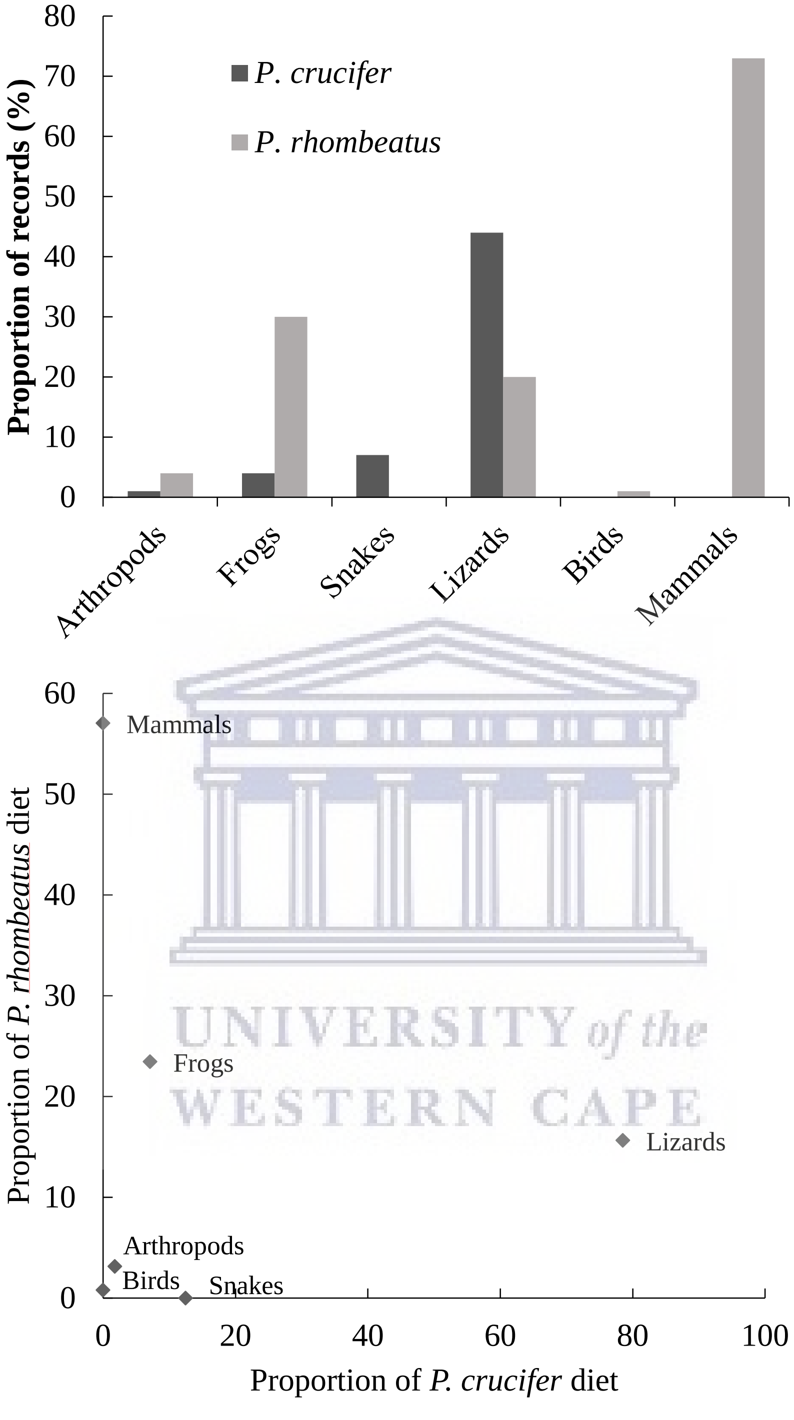

Figure 8: Proportion of known prey types in the diets of *P. rhombeatus* and *P. crucifer*. The top panel reflects these values for each species, whereas the bottom panel shows the relative abundances of each prey type when comparing between the species.

I performed a Spearman’s rank correlation analysis to test the hypothesis that the different prey types are represented proportionally in the diets of the two species. I found no relationship between the proportion of the prey types in the diets of the two species ($r = -0.20$; $p < 0.05$; Fig. 8: lower panel).

4. DISCUSSION

4.1. Niche partitioning in Psammophis crucifer and Psammophylax rhombeatus

I failed to detect any evidence of spatial niche differentiation between the two study species. Instead, my study found evidence to suggest the opposite, which is that the two species apparently respond similarly to their shared space and therefore do not partition spatial resources at this spatial scale. This finding was strongly, albeit circumstantially, supported across multiple analyses that revealed a constant pattern of a positive correlation in the abundance of the two species. Moreover, several best performing models of snake abundance included the abundance of a competitor. However, despite the crude but significant dietary similarities between these snakes as reflected in many field guides, a detailed analysis of their diet showed significant differences in what they eat. Taken together, these findings lead me to infer that these two snake species are able to co-exist because, despite a number of apparent ecological similarities, they partition food resources.

4.2. Scale appropriate spatial niche partitioning

Because of the broad scale congruence in their geographic distributions, it appears that these two snake species share spatial resources at very large spatial scales. For example, these two species both utilize grassland and fynbos habitats. My work to examine co-occurrence at a finer spatial scale found no evidence of spatial niche partitioning. In fact, my research found evidence to suggest that these two snakes share the same spatial resources across multiple spatial scales. This pattern might exist because fine scale spatial resources might not be limited for these species. This might be unsurprising given a lack of evidence for hibernacula or specialised nesting site usage in these species. Although such a pattern is likely common for many co-distributed organisms, studies that reveal such a pattern are rare. Rather, many species are co-distributed (and therefore share spatial resources at large spatial scales) but partition fine scale habitats to some degree. For example, Taniguchi and Nakamo (2000) showed that at landscape scales two salmonid fishes *Salvelinus malma* and *S. leucomaenis* co-occur in many streams in the Hokkaido Island in Japan, but exhibit fine scale spatial partitioning with *S. malma* predominantly occurring further up the stream, whereas *S. leucomaenis* occurs further downstream. Similar findings were found to occur in mosquitos that co-exist across multiple spatial scales, but show evidence of fine scale spatial partitioning (Laporta and Sallum, 2017).

*4.3 Is **Psammophylax rhombeatus** outcompeting **Psammophis crucifer**?*

It is possible that the relatively smaller numbers of *P. crucifer* captured in my study may reflect the result of competitive pressure exerted by *P. rhombeatus* (mostly for lizards, which appear to be more detectablein the landscape). It is worth highlighting the finding that *P. rhombeatus* was more abundant than *P. crucifer* in my capture sample. Although many studies were conducted on islands, interspecific competition is known to have fundamental ecological constraints on the abundance and distribution (Connell, 1961; Hairston, 1980; 1981) of sympatric species and has been documented across various taxa which includes small mammals (e.g., Crowell and Pimm, 1977), birds (e.g., Blondel *et al.*, 1988), lizards (e.g., Case and Bolger, 1991), arthropods (e.g., Greensdale 1971; Yamamoto *et al.,* 2007), fish (Taniguchi and Nakamo, 2000) and snakes (Luiselli, 2006a). Unfortunately, comparative measures of population densities for either snake species are not available in the literature to assess whether my estimated densities for *P. crucifer* are lower than on sites at which *P.*

rhombeatus is absent. One potential explanation is that *P. rhombeatus* has larger clutch sizes than *P. crucifer* and is therefore likely to be more r-selected. This might mean that *P. rhombeatus* could respond faster to changes in resource availability which might be happening if the system is not in equilibrium. In order to examine this idea I propose that future researchers find study sites in which one of the species is absent.

4.4. The low detection probability of snakes in Africa

I used several different approaches to try and quantify snake densities across sites for the two species. The reason for the many approaches to run the same analysis was deeply embedded in the fundamental challenge of low snake detection probability and the subsequent low captures. Thus although the data was collected over a relatively long duration, its quality was still poor and too sparse to build robust models such as the CJS to estimate population sizes.

The CJS method failed to successfully estimate population densities for neither study species. Model failure is usually accredited to convergence failure due to sparse data resulting from low capture rates (Pledger *et al.*, 2003). In the case of the current study, the convergence criteria were met for all models, yet, failed to estimate any of the parameters (population size, apparent survival, and capture probability) CJS estimates. I additionally tested model failure as a result of the data being too sparse by running test models. For each snake species, I pooled all capture data from all sampling sites and treated them as a single data set for one large sampling site. The test models were indeed successful in estimating all CJS parameters, thus confirming model failed was due to sparse data.

Upon further investigation attempting to find alternative methods to build the models, I was able to get some snake density estimates using the Royle-Nichols occupancy and Spatially Explicit Capture Recapture (SECR) approaches. Estimates from both analyses showed the same results. For some of the relatively better quality site-specific data, I was able to get some density estimates for both species. However, the highlight here was the apparent pattern whereby the raw count data showed the same pattern as the more complex analytical methods that were used, therefore suggesting with caution in worst case scenarios raw count data of unique individuals could be used to draw conclusions in future studies. Studies like the current one are important in the future, but people need to be aware of these challenges when they design and conduct similar investigations.

4.5. Design of future studies

Snakes are largely a difficult group to study because they exhibit cryptic behaviour, irregular activity patterns, and often occupy inaccessible places in their habitats (Parker *et al.*, 1987). Moreover, snake activity patterns are correlated to environmental conditions (Peterson *et al.*, 1993) so much that actively searching and capturing them may be subject to low capture rates with changing environmental conditions (Dorcas and Wilson, 2009). Because of these challenges, high resolution data about where wild snakes occur in their habitat is mostly lacking for many species (Jenkins *et al.*, 2009). When you combine all these snake-sampling related challenges and plan to do mark-recapture surveys, you really think about what you can do improve your sampling method to obtain good quality data when sampling.

Luiselli and Akani (1999) maximized their sampling effort by combining different methods to collect the same data. They selected ten 10 ha sites where they actively searched for snakes and also placed cover objects to flip and search for snakes. They also set up pitfall and funnel traps and additionally obtained samples from road kills and specimens provided to them by villagers and hunters. By doing all this, they were able to maximize their sampling effort and obtain high resolution data. The challenge of using all available methods to maximize effort is that studies become difficult to repeat and survey effort difficult to quantify However, the reality is that for many studies, the type of question you are trying to answer and hypothesis you are testing may dictate what you can or cannot employ in your survey method. The current study has maximized all sampling efforts to obtain high resolution mark-recapture data. Even though the current study data may well be the best of its kind in Africa to date, it still was not enough to successfully build complex CJS models.

The trapping system that was used in this study was selected because it had the most favourable and appropriate system for the kind of sampling that was needed to estimate snake densities in South Africa. One of the major advantages of using ACOs when trapping animals is that they facilitate free movement of animals in and out of the traps, therefore reducing the risk of them being vulnerable to potential threats like predation and environment stresses like desiccation. This trapping system by default allows long periods of time without needing to check traps and do much maintenance, except from the occasional loss of an ACO when seen by people or other large animals. Lastly, you could easily place your traps in any shape or size you deem more suitable for your study design.

In the current study, I used 600 x 600 mm plywood boards of which were set out in a grid form (see Fig. 4). This trapping method allows a lot of room for adjustment to maximise captures. One could adjust the size of the boards to larger sizes, but will have to be careful to not make them too big. Too big boards may very well be able to capture more individuals under a single board, but a board too large may make it difficult to capture small and fast animals who visit the boards during sampling. Ideally you could also have a fewer number of boards but larger board sizes, however this will still not resolve the issue of animals escaping.

Alternatively you could still have the desired cover board size, but increase the sampling area by adding more boards in the landscape. The boards could be placed within the existing design, therefore increasing board density and therefore increasing the animal-board encounter probability (Fig. 9). Additionally, you could increase the area being sampled by adding more rows of cover boards on the edges of the existing site design. Lastly and very important is the need to maximise and standardise sampling effort and intensity. In other words, you have to strictly adhere to the sampling protocol with regards to when you sample and also attempt to randomize the sampling order as this may be important for what animals you capture depending on the time or day. Moreover, if you do not remain consistent with the sampling effort, you may end up with difficulties when quantifying robust and complex analyses. Spatially explicit capture recapture models seem to be the best way to estimate snake densities because it uses animal capture histories as well as GPS co-ordinates for each of the cover boards.

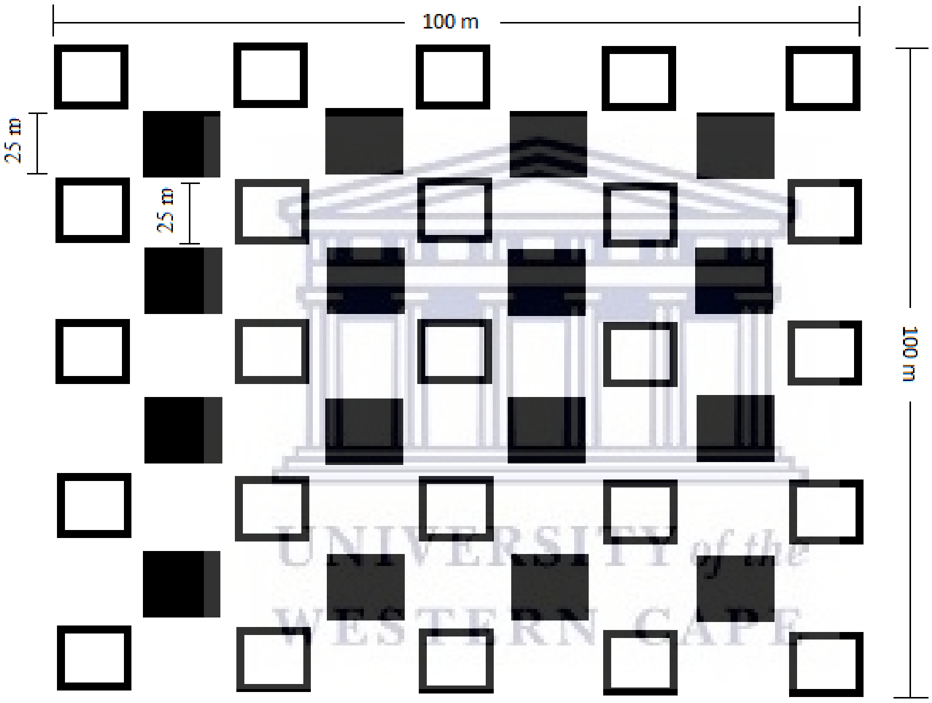

Figure 9: Proposed trapping design using ACO for estimating snake densities in future studies. White squares represent existing ACO layout; Black squares represent additional boards to be added.

4.6. Diet overlap

Although it is widely accepted that species of the genus *Psammophis* predominantly feed on lizards and that species of the genus *Psammophylax* predominantly feeds on frogs and mammals (Van Wyk, 1988; Douglas, 1992; Branch, 1998; Shine, 2006), detailed fine scale differences in their diets have not been measured, let alone compared at the scale and context of current study. My study found the same general feeding habits as reported in the literature. However, my study also shows fine scale dietary differences which may be facilitating the co-existence of these two snakes across multiple scales.

The diets of my study snakes are very similar because they predominantly consist of small vertebrates. However, a detailed Pianka's dietary niche overlap analysis showed that there are enough differences in their diet that they have very low dietary overlap of only 28%. This means at least 72 % of their diet is unique to either species. *Psammophylax rhombeatus* has a wider diet than *P. crucifer*, eating up to five of the six different prey types, but predominantly feeds on small mammals and frogs. Conversely, *P. crucifer* feeds only on four of the six types of prey and predominantly feeds on reptiles, however, lizards form bulk of their diet, thus making them more saurophagous snakes. My analysis, like many others, assumes that dietary records are drawn at random from the actual diet of the species. Unfortunately, it is unclear to what degree this assumption is met here. However, the fact that most diet records are from dissected museum specimens (Cottone and Bauer, 2010) means that dietary records are unlikely to be biased towards only novel prey items.

Despite there being a clear difference in the diet of these snakes, there are some clear overlaps in more commonly shared prey types. These include the diverse lizards, as well as the frogs. Competition for those shared resource may exist, and the intensity thereof may very temporally. Because prey availability and density can vary seasonally on the temporal scale (Luiselli, 2006c), ideally there is an expectation that predators dynamics may be indirectly influenced. In other words, you would expect a change in the intensity of competition between similar predators which share similar food resources depending on the availability and accessibility of said prey type. Similarly to the sympatric Afrotropical snakes (Luiselli, 2006b), ecologically similar snakes can continue feeding on the same prey types, but minimize their competition by feeding on different body sizes of that available prey sizes classes during seasons of high food scarcity in the landscape.

Larger bodied snakes tend to not only have wider diets, but also tend to feed on relatively larger prey as well (Akani *et al.,* 2003). For example, *Psammophis mossambicus* grows to be amongst the few large-bodied members of the psammophiine snakes who eat a wide variety of prey types which includes other snakes and mammal (Shine *et al.*, 2006). Similarly to *P. mossambicus*, *P. rhombeatus* has a relatively larger and more robust body type as compared to *P. crucifer* (Shine *et al.,* 2006; Cottone and Bauer, 2010). Because these snakes have evolved to be larger and subsequently broadening their diet by including larger prey types, I think it is plausible to speculate that there was a meaningful shift from the ‘ancestral’ or psammophiine characteristic saurophagus diet. Therefore, this leads me to think that the larger bodied members of the *Psammophylax* genus may have shifted their diet resulting in the dietary differences observed in my study. This in turn supports the wider diet which in turn facilitates co-existence between these two similar snakes across large and fine scales. Moreover, it advocates strongly for the wider diet of larger bodied *P. rhombeatus* which include the additional larger prey types consisting of birds and small mammals. This within itself contributes to reducing the suite of interspecific factors that would otherwise intensify competition for the acquisition of shared food resources between *P. crucifer* and *P. rhombeatus*. The findings in this study corresponds to the general patterns associated with temperate regions, whereby snake communities are known to partition food resources in areas of overlap (Seigel *et al.,* 1987).

Intra-guild predation basically refers to those species that share the same class of environmental resources, but may also fall prey to each other within that shared environment (Polis *et al.,* 1989). Snake-eating in psammophiids is not uncommon (Schleich *et al.,* 1996; Akani *et al.,* 2003; Shine, 2006). However, it is interesting to see *P. crucifer* also included in that group of ophidian psammophiids especially because ophidian feeding habits have been mainly associated and recorded for larger bodied psammophiids (Schleich *et al.*, 1996; Akani *et al.*, 2003; Shine, 2006). Nonetheless, there are several records of this snake eating other snake species like sympatric congeneric *Psammophis* spp., *Philothamnus natalensis*, *Duberria lutrix*, and *P. rhombeatus*. However, the highlight for the current study is the apparent intra-guild predation that is occasionally observed with *P. crucifer* preying on *P. rhombeatus*. Also contributing to ephemeral intra-guild predation events being rarely observed could habitat heterogeneity which can reduce predator (*P. crucifer*) prey (*P. rhombeatus*) encounter. During the course of the current study, I encountered both species under the same ACO on multiple occasions (Fig. 10, top), suggesting maybe the habitat heterogeneity may not be that effective in my study system especially given that these snakes spatially respond similarly in their habitats.

Figure 10: Both species occupying the same ACO (top). Intra-guild predation, big *P. crucifer* eating a small *P. rhombeatus* (bottom). Photo cred: Hannelie Fourie Coetzee. Source: Facebook group Predation Records: Reptiles and Frogs (Sub-Saharan Africa).

Moreover, considering the reality that adult *P. crucifer* are smaller compared to adult *P. rhombeatus*, big *P. crucifer* may be feeding on small *P. rhombeatus* when these ephemeral intra-guild predation events occur (Fig. 10, bottom). In the case of this study, I conclude that *P. crucifer* and *P. rhombeatus* are able to coexist across multiple scales because they have strong dietary niche differentiation where they occur sympatrically.

Studies concerning snake population dynamics are rare in Africa and most of the existing studies are dominated by European and North American examples (Shine *et al.*, 1998; Maritz and Alexander, 2012). This makes it difficult to compare and draw conclusion across these snake communities, especially because of the geographic extent and the unique African reptile diversity. Because snakes tend to be cryptic and depict low detectability, this often makes studying their population dynamics difficult, especially because such robust analysis require relatively large good quality data (Parker and Plummer, 1987). This really contributes to the underrepresentation of snake population ecology (Parker and Plummer, 1987; Shine *et al.*, 1998; Bonnet *et al.*, 2002). Of the existing studies that have estimated snake populations, fewer have used mark-recapture models (Koons *et al.*, 2009) and the current study demonstrates just how difficult it can be to produce these robust empirical estimates as a result of having sparse data. In fact, with the exception of the current study, there are about four African examples that used mark-recapture for estimating snake population densities. These include earlier work on *Lycodonomorphus bicolor* in Lake Tanganyika, Zambia (Madsen and Osterkamp, 1982); more recent work in West Africa on the large viper species *Bitis nasicornis* and *Bitis gabonica* (Luiselli, 2006c), and lastly on the smallest viper *Bitis schneideri* in the west coast of South Africa (Maritz and Alexander, 2012).

I the current study, three of the four methods used to estimate snake densities were able to produce some estimates for some sites, for both species. Using the averages of the estimated snake densities from each analysis I can then summarise and compare the numbers of *P. rhombeatus* to *P. crucifer* per hectare (~ha^{-1}). Here I show that (1) Raw count data estimated 6 and 4, (2) RN estimated 48 and 53, and lastly (3) SECR estimated 4 and 6. Note that the estimates for the SECR have been refined from number of individuals in 9 hectares to the number of individuals per hectare. Because studies showing snake densities in Africa are rare (Parker and Plummer, 1987), it is challenging to compare my findings to similar species. Of the very few African examples that quantified snake densities, we find that they are dominated by members representing viper species namely *Bitis gabonica* and *B. nasicornis*

(Luiselli, 2006c), *Dendroaspis jamesonii* (Luiselli, 2000), and *B. schneideri* (Maritz and Alexander, 2012). Madsen and Ostercamp (1982) are the only ones to measure snake density in a member of Lamprophiidae in African species. In their study, they estimated densities up to 380 ha^{-1}for *Lycodonomorphus bicolor* in spite of Janzen's (1976) speculation that Africa may have low abundance. The current study additionally shows a clear example of relatively high abundance of snakes in Africa.

In South Africa alone, we have a highly diverse group of snakes and the numerous varieties within Psammophiidae alone may well serve to emphasize that. Apart from the current study species, there remains opportunity to ask the same questions as in the current study with other candidate species that are ecologically and biologically similar. For example, someone could investigate dietary overlap in *Psammophis notostictus* and *Psammophis leightoni*. Or even quantify and compare dietary differences in the sympatric species of genus *Dasypeltis* in the Kwazulu-Natal province.

5. Conclusions

The two phylogenetically closely related species co-occur at the broad spatial scales and share a number of attributes. An extensive data set of 96 captures over four years provided string circumstantial support for the idea that their abundance are positively correlated meaning that they are not partitioning space across large geographic and localized fine-scales. Unfortunately several of the approaches that I used were still not sensitive enough to provide robust empirical estimates of abundance because of the low recapture rates. However, dietary analysis revealed important differences in the diets of the two species, suggesting that the niche partitioning is likely being facilitated at local and broad scales by difference in food resources.

6. REFERENCES

Abzhanov, A., Protas, M., Grant, B.R., Grant, P.R., and Tabin, C.J. (2004) Bmp4 and Morphological Variation of Beaks in Darwin's Finches. Science, 305:1462–1465.

Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. 267–281 in B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.

Akani, G.C., Eniang, E.A., Ekpo, I.J., Angelici, F.M., and Luiselli, L. (2003) Food habits of the snake *Psammophis phillipsi* from the continuous rain-forest region of southern Nigeria (West Africa). Journal of Herpetology, 37:208–211.

Akani, G.C., Politano, E., and Luiselli, L. (2004) Amphibians recorded in forest swamp areas of the River Niger Delta (south-eastern Nigeria), and the effects of habitat alteration from oil industry development on species richness and diversity. Applied Herpetology, 2:1–22.

Alexander, G., and Marais, J. (2007) A guide to the reptiles of southern Africa. Struik Nature, Penguin Random House South Africa.

Amstrup, S.C., McDonald, T.L., and Manly, B.F. (eds). (2010) Handbook of capture-recapture analysis. Princeton University Press.

Andreone, F., and 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? Review of Ecology, 55:215–239.

Angelici, F.M., and Luiselli, L. (2005) Patterns of specific diversity and population size in small mammals from arboreal and ground-dwelling guilds of a forest area in southern Nigeria. Journal of Zoology, 265:9–16.

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

Begon, M., Townsend, C.R., and Harper, J.L. (2006) Ecology: From individuals to ecosystems, 4th ed, Blackwell Publishing Ltd, UK.

Blondel, J., Chesset, B., and Frochot, D. (1988) Bird species impoverishment, niche expansion, and density inflation in Mediterranean island habitats. Ecology, 69:1899–1917.

Böhm, M., Collen, B., Baillie, J.E., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M., and Rhodin, A.G. (2013) The conservation status of the world’s reptiles. Biological Conservation, 157:372-385.

Bombi, P., Luiselli, L., Capula, M., and Salvi, D. (2009) Predicting elusiveness: potential distribution model of the Southern smooth snake. *Coronella girondica*, in Italy. Acta Herpetologica, 4:7–13.

Bonnet, X., Pearson, D., Ladyman, M., Lourdais, O.. and Bradshaw, D., (2002) ‘Heaven’for serpents? A mark–recapture study of tiger snakes (*Notechis scutatus*) on Carnac Island, Western Australia. Austral Ecology, 27(4):442–450.

Branch, W.R. (1998) A Field Guide to Snakes and Other Reptiles of Southern Africa. Third edition. Struik Publishing, Cape Town.

Branch, W.R., and Bauer, A.M., (1995) Herpetofauna of the Little Karoo. Western Cape.

Branch, W.R., and Braack, H.H., (1987) Reptiles and amphibians of the Addo Elephant National Park. Koedoe, 30(1):61-111.

Branch, W.R., Baptista, N., Keates, C., and Edwards, S. (2019) Rediscovery, taxonomic status, and phylogenetic relationships of two rare and endemic snakes (Serpentes: Psammophiinae) from the southwestern Angolan plateau. Zootaxa, 459:342–366.

Broadley, D.G. (1966) The herpetology of south-east Africa (Doctoral dissertation).

Broadley, D.G. (1977) A revision of the African snakes of the genus *Psammophylax* Fitzinger (Colubridae). National Museums and Monuments of Rhodesia, 6:1– 44.

Broadley, D.G. (2002) A review of the species of *Psammophis* Boie found south of Latitude 12uS (Serpentes: Psammophiinae). African Journal of Herpetology, 51:83–119.

Burnham, K.P., and Anderson, D.R. (1998) Model selection and inference: A practical information-theoratical approach. New York: Springer-Verlag.

Case, T.J., and Bolger, D.T. (1991) The role of interspecific competition in the biogeography of island lizards. Trends in Ecology and Evolution, 6:135–139.

Connell, J.H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology, 42:710–723.

Corrêa, C.E., Albrecht, M.P., and Hahn, N.S. (2011) Patterns of niche breadth and feeding overlap of the fish fauna in the seasonal Brazilian Pantanal, Cuiaba´ River basin. Neotrop ichthyol.

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

Cottone, A.M., and 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, 4:578–590.

Crowell, K.L., and Pimm, S.L. (1977) Competition and niche shifts of mice introduced onto small islands. Oikos, 27:251–258.

Da Silva, J.C., Gubiani, É.A., Neves, M.P., and Delariva, R.L. (2017) Coexisting small fish species in lotic neotropical environments: evidence of trophic niche differentiation. Aquatic Ecology, 51(2):275–288.

De Haan, C.C. (2003) Extrabuccal infralabial secretion outlets in *Dromophis*, *Mimophis*, and *Psammophis* species (Serpentes, Colubridae, Psammophiini). A probable substitute for ‘‘self-rubbing’’ and cloacal scent gland functions, and a cue for a taxonomic account. Comptes Rendus Biologies, 36:275–286.

De Waal, S.W.P. (1977) The Squamata (Reptilia) of the Orange Free State, South Africa (Doctoral dissertation).

Denman, K.L.. and Platt, T. (1975) Coherences in the horizontal distributions of phytoplankton and temperature in the upper ocean. Memoirs Societie Royal Science Liege (Series 6), 7:19–36.

Dorcas, M.E., and Willson, J.D. (2009) Innovative Methods for Studies of Snake Ecology and Conservation. Ecology and Conservation, 5.

Douglas, A.M. (1990) Volume determination of reptilian and avian eggs with practical applications. South African Journal of Wildlife Research-24-month delayed open access, 20(3):111–117.

Efford, M. (2015). secr 2.9-spatially explicit capture–recapture in R.

FitzSimons, V. (1935) Notes on a collection of reptiles and amphibians made in the southern Kalahari, Bushmanland and Great and Little Namaqualand. Annals of the Transvaal Museum, 15(4):519–550.

FitzSimons, V.F.M. (1962) Snakes of Southern Africa. Snakes of Southern Africa.

Gause, G.F. (1934) The Struggle for Existence. Williams & Wilkins, Baltimore (reprinted 1964 by Hafner, New York).

Goodyear, S.E., and Pianka, E.R. (2008) Sympatric ecology of five species of fossorial snakes (Elapidae) in Western Australia. Journal of Herpetology, 42(2):279–285.

Gotelli, N.J., and Entsminger, G.L. (2006) EcoSim: null models software for ecology. Acquired Intelligence Inc. & Kesey-Bear.

Greensdale, P.J.M. (1971) Interspecific competition and frequency changes among ants in Solomon Islands coconut plantations. Journal of Applied Ecology, 8:323–352.

Grossman, G.D. (1986) Food resources partitioning in a rocky intertidal fish assemblage. Journal of Zoology, 1:317–355.

Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N., Lehmann, A., and Zimmermann, N. (2006) Using Niche-Based Models to Improve the Sampling of Rare Species. Conservation Biology, 20:501–511.

Haagner, G.V., and Branch, W.R. (1993) *Psammophis crucifer*, Cross-marked sand snake: diet. Journal of the Herpetological Association of Africa, 42:39.

Hairston, N. (1980) The experimental test of an analysis of field distributions: Competition in terrestrial salamanders. Ecology, 61:817–826.

Hairston, N.G. (1981) An experimental test of a guild: salamander competition.

Ecology, 62(1):65–72.

Janzen, D.H. (1976) The depression of reptile biomass by large herbivores. The American Naturalist, 110(973):371–400.

Jenkins, C.L., Peterson, C.R., Doering, S.C., and Cobb, V.A. (2009) Microgeographic variation in reproductive characteristics among western rattlesnake (*Crotalus oreganus*) populations. Copeia, 2009(4):774–780.

Keates, C., Conradie, W., Greenbaum, E. and Edwards, S. (2019) A snake in the grass: Genetic structuring of the widespread African grass snake (*Psammophylax* Fitzinger 1843), with the description of a new genus and a new species. Journal of Zoological Systematics and Evolutionary Research, 57(4):1039–1066.

Kelly, C.M.R., Barker, N.P., Villet, M.H., Broadley, D.H., and 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.

Koons, D.N., Birkhead, R.D., Boback, S.M., Williams, M.I., and Greene. M.P. (2009) The effect of body size on Cottonmouth (*Agkistrodon piscivorus*) survival, recapture probability, and behavior in an Alabama swamp. Herpetological Conservation and Biology, 4:221–235.

Krebs, C.J. (1972) The experimental analysis of distribution and abundance. Ecology. New York: Harper and Row, 1–14.

Laporta, G.Z. and Sallum, M.A.M. (2014) Coexistence mechanisms at multiple scales in mosquito assemblages. BMC Ecology, 14(1):30.

Le Roux, C. (2014) Koeberg Nature Reserve Management Plan. Revision 0.159.

Linder, H.P. (2003) The radiation of the Cape flora, southern Africa. Biological Reviews, 78, 597–638.

Linder, H.P., Johnson, S. D., Kuhlmann, M., Matthee, C. A., Nyffeler, R., and Swartz, E. R. (2010) Biotic diversity in the Southern African winter-rainfall region. Current opinion in environmental sustainability, 2:109–116.

Lotka, A.H. (1932) The growth of mixed populations: two species competing for a common food supply. Journal of the Washington Academy of Sciences, 22:461–469.

Love, T.F. (1977) Ecological niche theory in sociocultural anthropology: a conceptual framework and an application 1. American Ethnologist, 4(1):27–41.

Luiselli, L. (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, 81:228–236.

Luiselli, L. (2006a) Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. Oikos, 114:193–211.

Luiselli, L. (2006b). Interspecific relationships between two species of sympatric Afrotropical water snake in relation to a seasonally fluctuating food resource. Journal of Tropical Ecology, 22: 91–100.

Luiselli, L. (2006c) Site occupancy and density of sympatric Gaboon viper (*Bitis gabonica*) and Nose-horned viper (*Bitis nasicornis*). Journal of Tropical Ecology, 22:555–564.

Luiselli, L. Akani, G. C. and Capizzi, D. (1998) Food resource partitioning of a community of snakes in a swamp rainforest of south-eastern Nigeria. Journal of Zoology, 246:125–133.

Luiselli, L. and Angelici, F.M., 2000. Ecological relationships in two Afrotropical cobra species (*Naja melanoleuca* and *Naja nigricolli*s). Canadian Journal of Zoology, 78(2):191–198.

Luiselli, L., and Akani, G. C. (2003) Diet of sympatric Gaboon vipers (*Bitis gabonica*) and nose-horned vipers (*Bitis nasicornis*) in southern Nigeria. African Journal of Herpetology, 52:101–106.

Luiselli, L., and Akani, G.C. (2002) An investigation into the composition, complexity and functioning of snake communities in the mangroves of south-eastern Nigeria. African Journal of Ecology, 40:220–227.

Luiselli, L., Angelici, F.M., and. Akani. G.C. (2000) Large elapids and arboreality: The ecology of Jameson's green mamba (*Dendroaspis jamesoni*) in an Afro-tropical forested region. Contributions to Zoology, 69:1–11.

Luiselli, L., Capula, M., Rugiero, L., Salvi, D. and Akani, G. (2012) Does interspecific competition with a stronger competitor explain the rarity of an endangered snake on a Mediterranean island? Ecological Research, 27(3):649–655.

Luiselli, L., E. Filippi, and M. Capula. (2005) Geographic variation in diet composition of the grass snake (*Natrix natrix*) along the mainland and an island of Italy: the effects of habitat type and interference with potential competitors. Herpetological Journal, 15:221–230.

Luiselli, L., and Akani, G. C. (1999) Habitats of snakes in the rainforests of Eket (Akwa-Ibom State, south–eastern Nigeria). Herpetozoa, 11:99–107.

MacArthur, R., and Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist, 101(921):377–385.

Madsen, T., and Osterkamp, M. (1982) Notes on the biology of the fish-eating snake *Lycodonomorphus bicolor* in Lake Tanganyika. Journal of Herpetology, 16:185–188.

Maritz, B. (2011) Ecology of the Namaqua Dwarf Adder, Bitis scheideri. PhD thesis, University of the Witwatersrand, Johannesburg, South Africa.

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

Maritz, B., Verbugt, L., Coetzer, A., Ping, T., Maritz, R.A., Nicholau, G., Parry N., and Boyce, J. (2020) Facebook group: Predation records—reptiles and frogs. https://web.facebook.com/groups/888525291183325/.

Maritz, R. A., and Maritz, B. (2020) Sharing for science: high-resolution trophic interactions revealed rapidly by social media. PeerJ, 8:9485.

Martin, P.R., and Martin, T.E. (2001) Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. Ecology, 82, 189–206.

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

Park, T. (1962) Beetles, competition, and populations. Science, 138:1369–1375.

Parker, W.S., Plummer, M.V., Siegel, R.A., Collins, J.T. and Novak, S.S. (1987)

Snakes: ecology and evolutionary biology. McMillan, New York, 253–301.

Perkins, M.W., Cloyed, C.S., and Eason, P.K. (2020) Intraspecific dietary variation in niche partitioning within a community of ecologically similar snakes. Evolutionary Ecology, 1–19.

Peters, R.H. (1983) The ecological implications of body size. Cambridge University Press, Cambridge.

Peterson, C. R., Gibson, A. R., and Dorcas, M.E. (1993) Snake thermal ecology: The causes and consequences of body-temperature variation. 241–314. In Seigel, R. A., and Collins, J. T. (Eds.), Snakes: Ecology and Behavior. McGraw-Hill, New York, New York, U.S.A.

Pianka, E.R., (1974). Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences, 71(5):2141–2145.

Pietro, D.O., Williams, J.D., Cabrera, M.R., Alcalde, L., Cajade, R. and Kacoliris, F.P. (2020) Resource partitioning in a snake assemblage from east-central Argentina. Anais da Academia Brasileira de Ciências. 92(2).

Pledger, S., Pollock, K., and Norris, J. (2003) Open Capture-Recapture Models with Heterogeneity: I. Cormack-Jolly-Seber Model. Biometrics, 59(4):786–794.

Plummer, M.V., and Ferner, J.W. (2012) Marking Reptiles. *In*: Reptile Biodiversity: Standard Methods for Inventory and Monitoring. University of California Press. 143–150.

Polis, G.A., Myers, C.A., and Holt, R.D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual review of ecology and systematics, 20(1):297–330.

R core team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing', https://www.r-project.org.

Rahman, S.C., Reza, A.A., Datta, R., Jenkins, C.L. and Luiselli, L. (2014). Niche partitioning and population structure of sympatric mud snakes (Homalopsidae) from Bangladesh. The Herpetological Journal, 24(2):123–128.

Schleich, H.H., Kästle, W., and Kabisch, K. (1996) Amphibians and reptiles of North Africa (Vol. 63). Germany: Koeltz scientific books, Koenigstein.

Schoener, T.W. (1983) Field experiments on interspecific competition. The American Naturalist, 122(2):240–285.

Schoener, T.W., (1974). Resource partitioning in ecological communities. Science, 185(4145):27–39.

Schönland, J. (1895). Snake Cannibalism. Nature, 51(1326):511-511.

Seigel, R.A., Collins, J.T., and Novak, S.S. eds., (1987) Snakes: ecology and evolutionary biology. USA: Macmillan.

Shine, R., Branch, W.R., Harlow, P.S., Webb, J.K., and Shine, T. (2006) Sexual dimorphism, reproductive biology, and dietary habits of psammophiine snakes (Colubridae) from southern Africa. Copeia, 650–664.

Shine, R., W.R. Branch, P.S. Harlow, and J.K. Webb. 1998. Reproductive biology and food habits of Horned Adders, *Bitis caudalis* (Viperidae), from southern Africa. Copeia, 1998:391–401.

Shroener, T.W. (1973) Population growth regulated by interspecific competition for energy or time: some simple representations. Theoretical Population Biology, 4:56–84.

Shroener, T.W. (1983) Field experiments on interspecific competition. American Naturalist, 122:240–285.

Steen, D.A., McClure, C.J., Brock, J.C., Craig Rudolph, D., Pierce, J.B., Lee, J.R., Jeffrey Humphries, W., Gregory, B.B., Sutton, W.B., Smith, L.L., and Baxley, D.L. (2014) Snake co-occurrence patterns are best explained by habitat and hypothesized effects of interspecific interactions. Journal of Animal Ecology, 83(1):286–295.

Taniguchi, Y., and Nakano, S. (2000) Condition-specific competition: implications for the altitudinal distribution of stream fishes. Ecology, 81:2027–2039.

Tansley, A.G., (1917) On competition between *Galium saxatile* L.(*G. hercynicum* Weig.) and *Galium sylvestre* Poll.(*G. asperum* Schreb.) on different types of soil. The Journal of Ecology, 173–179.

Teixeira, C., Montag, L.F., and Santos-Costa, M.C. (2017) Diet composition and foraging habitat use by three species of water snakes, *Helicops* Wagler, 1830,(Serpentes: Dipsadidae) in eastern Brazilian Amazonia. Journal of Herpetology, 51(2):215–222.

Tilman, D., Mattson, M., and Langer, S. (1981) Competition and nutrient kinetics along a temperature gradient: an experimental test of a mechanistic approach to niche theory. Limnology and Oceanography, 26:1020–1033.

Toft, C. (1985) Resource Partitioning in Amphibians and Reptiles. Copeia, 1–21.

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

Van Wyk, J.H. (1988) The diet of the Rhombic Skaapsteker, *Psammophylax r. rhombeatus*: results. Navorsinge van die Nasionale Museum: Researches of the National Museum, 5(16):456–458.

Vidal, N., Branch, W., Pauwels, O., Hedges, S., Broadley, D., Wink, M., Cruaud, C., Joger, U., and Nagy, Z. (2008) Dissecting the major African snake radiation: a molecular phylogeny of the Lamprophiidae Fitzinger (Serpentes, Caenophidia). Zootaxa, 1945(1), 51–66.

Yamamoto, N., Yokoyama, J., and Kawata, M. (2007) Relative resource abundance explains butterfly biodiversity in island communities. Proceedings of the National Academy of Sciences, 104:10524–10529.