GEOGRAPHIC DISTRIBUTION AND HABITAT SELECTION IN THE BERG ADDER, *BITIS ATROPOS* (SERPENTES, VIPERIDAE) ON THE MPUMALANGA ESCARPMENT, AND THE CONSEQUENCES FOR CONSERVATION

Submitted by

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Submitted in fulfillment of the requirements for the Degree of Magister Scientiae in Department of Zoology and Entomology in the Faculty of Natural and Agricultural Sciences at the University of the Free State Bloemfontein, South Africa

June 2019

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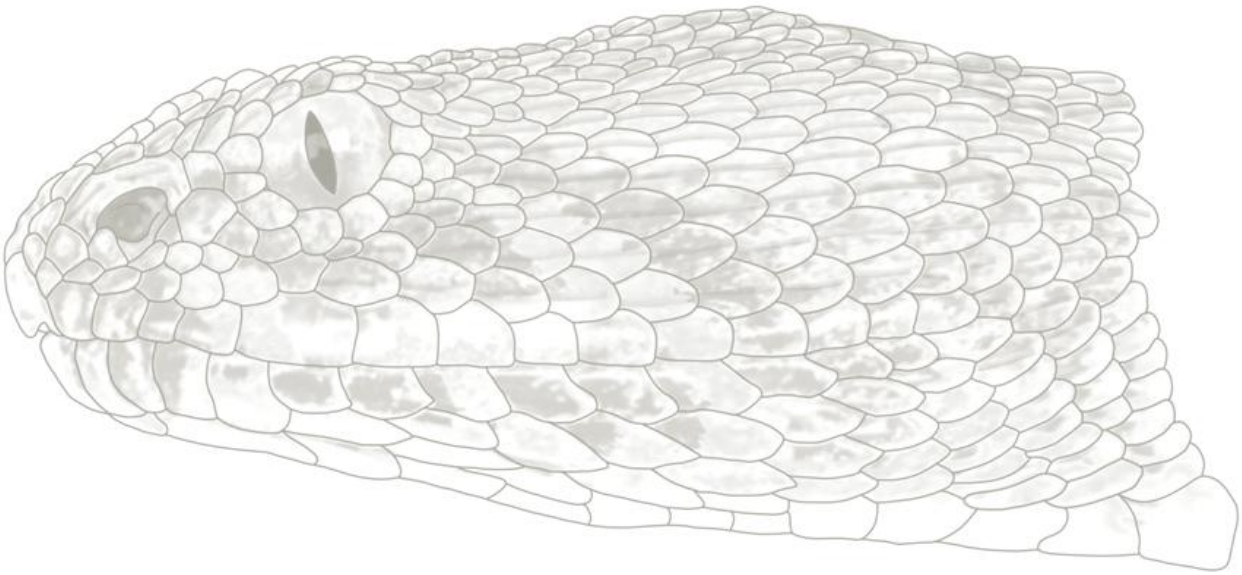
DECLARATION



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I, **Adriaan Jordaan**, declare that the Master's Degree research dissertation that I herewith submit for the Master's Degree qualification in **Zoology** at the University of the Free State is my independent work, and that I have not previously submitted it for a qualification at another institution of higher education.

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Adriaan Jordaan Date

"…successful research doesn't depend on mathematical skill, or even deep understanding of theory. It depends on large degree on choosing an important problem and finding a way to solve it, even imperfectly at first. Very often ambition and entrepreneurial drive, in combination, beat brilliance."

- **Edward O. Wilson, *Letters to a young scientist***

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ABSTRACT

Understanding how species use geographic space is foundational to ecology, biogeography and conservation biology. However, such essential geographic information remains unavailable for many species. This is especially true for reptiles, which, despite being the largest group of terrestrial vertebrates, remain poorly studied relative to other groups. Moreover, the number of reptile species keeps growing, as new species are discovered and described from existing species complexes. Therefore, in this dissertation, I set out to narrow this knowledge-gap by exploring geographic patterns in the Mpumalanga population of the berg adder (*Bitis atropos*). This population represents a distinct evolutionary lineage within a larger species complex and justifies reconsideration as a distinct species. I began by using species distribution modelling to estimate the total geographic range size of this snake lineage and showed how it has a restricted distribution that has experienced persistent habitat loss in recent decades. Combined, these results suggest that this lineage would be classified as "Vulnerable" according to IUCN criteria should it be recognised as a new species. I then carried out repeated field surveys to study Mpumalanga berg adder habitat-use within the Buffelskloof Private Nature Reserve. These field records were combined with topographic information to quantify habitat occupancy and account for imperfect detection. Analyses showed that the snakes were more likely to occur on north-west facing slopes with higher heat load index values and, therefore, higher ambient energy. This is important for behavioural thermoregulation in ectothermic species. By understanding distribution patterns and habitat use, this thesis is an important piece in a

larger puzzle of reptile spatial ecology. Ultimately, the results presented here provide a deeper evidence base on the ecology and biogeography of a poorly-studied reptile to inform future conservation and management.

Keywords: *Bitis atropos;* conservation*;* distribution patterns; habitat use; occupancy; reptiles; species distribution modelling.

ACKNOWLEDGEMENTS

Studying snakes under natural field conditions has always been a dream of mine. Having the opportunity to study my favourite snake species in what is probably my favourite environmental setting – mountains – was, to say the least, an amazing experience. In the mountains, I experienced wilderness for the first time and was excited to see wildlife that I had observed countless times before, with the difference that they were actually wild – unconstrained by arbitrary, man-made boundaries, free to come and go as they pleased in a place where nature seemed independent of human intervention. For this experience, I have many people to thank.

To my supervisors, Dr Falko Buschke and Prof. Neil Heideman, thank you for giving me this opportunity and guiding me throughout the process. I genuinely appreciate it. Furthermore, Prof. Neil, thank you for always trusting and believing in me. From the day I met you, you always let me follow my own path, and for that I'm truly grateful. Dr Falko Buschke, thank you for the time, effort and patience you spent on making this project a success. More than that, thank you for mentoring me; you have shown me that I'm capable of much more than I had previously imagined. Lastly, thank you for instilling in me an even greater love of ecology and conservation. The scientific and philosophical inspiration you gave me will persist for a lifetime, so, again, thank you, Falko.

To the special people of Buffelskloof, thank you so much for accommodating me on my extended fieldwork visits; without your continued logistical and moral support, this project could never have been completed. John and Sandy, there are no words to

describe how lucky I was to carry out my research at such an extraordinary place as your home. Furthermore, John, thank you for all the discussions of topics related to natural history and for your continued interest in my research. The same gratitude is due to Sandy. You tolerated the often prolonged jibber-jabber between John and me, and your love and appreciation of nature is as admirable as your skilled botanical artistry! To Barbara Turpin, thank you for keeping me alive with your frequent and wonderful cooking and for trusting me to look after Cleo when you were not around. Also, thank you for helping me with fieldwork and teaching me about the smaller, lesser-known plants; genera such as *Hypoestes, Commelina,* and *Aneilema* will remain forever etched in memory. I truly appreciate everything you have done for me. Finally, I thank the Pretorius family – Pieter, Jennie and Josh – for their hospitality and for always forwarding interesting reptile pictures to me. Additionally, thank you, Pieter, for taking the time to explain some of the nuances of reading tracks and signs.

To Luke, Ursula and Leela Verburgt (Enviro-Insight), thank you! You become great friends and were always willing to go above and beyond the call of duty to provide help, whether scientific or personal. You guys remained supportive and were awesome companions in the field.

I thank the following individuals for fieldwork assistance: Johan Marais (African Snakebite Institute), Eulalia Jordaan (North-West University) Gary Kyle Nicolau (Rhodes University), Prof. Amos Bouskila (Ben-Gurion University), Prof. Aaron Bauer (Villanova University), Dr Luis Ceríaco (Villanova University), Suzanna Bandeira, Dr Tania Bird (Ben-Gurion University), Gal Kagan, Horst Filter, Prof. Willem Ferguson (University of Pretoria), Dr Joaquín Verdú-Ricoy (University of the Free State) and

Gideon and Jessie de Villiers. Gary Kyle Nicolau is also thanked for the berg adder illustration.

I also wish to thank my lab mates, Antón, Joaquín, Zhao and Sinalo, for moral support and academic input.

I thank Mr Hennie Butler (University of the Free State) for going out of his way to support me with extra equipment. To Dr Mike Bates (National Museum Bloemfontein), thanks for your help at the inception of this project; I always look forward to your advice and general discussions.

Financial assistance from the National Research Foundation (NRF) is hereby acknowledged. I am grateful to the NRF for awarding Adriaan Jordaan an Innovation and Scarce Skills Development Masters Scholarship and for providing funding to Prof. Neil Heideman (grant no. IFR150216114248). Permission to carry out this research was obtained from the Mpumalanga Tourism and Parks Agency (MTPA) under permit no. MPB. 5571/2, and ethical clearance was provided by the University of the Free State's Animal Ethics Committee (clearance no. UFS-AED2016/0115). I also wish to extend my sincere gratitude to Dr Mervyn Lotter and Dr Hannes Botha of the MTPA for their willingness to help and for sharing locality information.

Last but not least, I thank my parents for supporting me throughout my academic journey; your love and support is much appreciated! To Simonet, thank you for everything. It was absolutely delightful to have you in the field with me, and I appreciate everything you do and have done for me!

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AUC -Area under the curve

BKPNR -Buffelskloof Private Nature Reserve

CR -Critically Endangered

CTI -Compound Topographic Index

DEA -Department of Environmental Affairs

DEM -Digital Elevation Model

ELEV -Elevation

ELSQ -Elevation-Squared

EN -Endangered

EOO -Extent of Occurrence

EquSS -Equal Training Sensitivity and Specificity

HLI -Heat Load Index

IUCN -International Union for Conservation of Nature

MaxSS -Maximum Training Sensitivity plus Specificity

MTP -Minimum Training Presence

MTPA -Mpumalanga Tourism and Parks Agency

PA -Protected Area

ROC -Receiver Operating Characteristic

SDM -Species Distribution Modelling

SLO -Slope

SRTM -Shuttle Radar Topography Mission

TPI -Topographic Position Index

TSS -True Skill Statistic

VRM -Vector Ruggedness Measure

VU -Vulnerable

WDPA -World Database on Protected Areas

CHAPTER 1: General Introduction

Knowledge gaps in reptile ecology

Understanding species' distribution patterns and habitat preferences are fundamental for assessing extinction risk and for guiding conservation actions (Frey *et al.* 2012; Gadenne *et al*. 2014; Hortal *et al.* 2015). This becomes a considerable challenge for species that are regarded as difficult to study due to their intrinsic and extrinsic biological traits, are generally perceived negatively by the public, or contain a large number of undiscovered or undescribed cryptic species (Lyet *et al.* 2013; Meiri & Chapple 2016). This is especially true for reptiles, which remain poorly studied compared to other vertebrate classes despite being the most diverse terrestrial vertebrate class (Tingley *et al.* 2016; Roll *et al.* 2017). This contributes to reptiles often being excluded from conservation prioritizations even when they are suffering global population declines (Gibbons *et al.* 2000; Roll *et al.* 2017; Tolley *et al.* 2019).

A contributing factor to the reptile knowledge-gap is the rapidly growing number of species known to science (Meiri 2016). This is partly due to the discovery of new reptile species, but also the description of new species from existing species complexes due to modern taxonomic and molecular techniques (Böhm *et al.* 2013; Meiri & Chapple 2016). This has meant that the description of new reptile species is outpacing the conservation assessments that evaluate these species' extinction risks (Meiri 2016; Meiri & Chapple 2016).

Unsurprisingly, global evaluations of reptiles' extinction risks lag behind those of other terrestrial vertebrate groups and are almost exclusively based on estimates of

geographic range size due to the challenges of collecting fine-scale data related to species' habitat preferences (Böhm *et al.* 2013; Meiri & Chapple 2016). Nevertheless, the drivers of species occurrence patterns at local scales are important for mitigating reptile extinctions (Böhm *et al.* 2013; Tolley *et al.* 2019). Threatening processes that exacerbate species extinction risk may be scale-dependent because threats perceived as unimportant across the entire geographic distribution of a species might be an important factor limiting species survival and persistence at the population level (Habel *et al.* 2013). This emphasizes the importance of studying reptile distributions across different spatial scales.

The challenge, therefore, lies in merging information on distributions across scales. It is important to understand range-wide distribution patterns to place the species' in a global context of extinction risk. This should be coupled to knowledge relating to species habitat preferences at the local scale, so that reserve managers, for example, are able to incorporate reptiles into their existing conservation management plans. Consequently, to close the knowledge gap of reptile ecology, global reptile conservation should encourage a multi-scale approach that explicitly quantify species habitat requirements at the scale of local populations as well as the scale of the entire species' geographic range.

Shedding light on the Dark Continent

Even though reptiles are poorly studied globally, certain geographic regions are better studied than others (Tolley *et al.* 2016). Reptiles species from regions characterized by historical socio-economic instability, such as Africa, are particularly understudied and

suffer from incomplete taxonomic and geographic knowledge (Balmford *et al.* 2001; Tolley *et al.* 2016; Tolley *et al.* 2019). Although recent efforts have made considerable progress in mapping African reptile distributions (e.g. Lewin *et al.* 2016), there is still a shortfall of detailed geographic information per species. Although mainland Africa together with Madagascar contains *ca.* 20% of the world's reptile fauna, the number of distribution records per species is disproportionately lower than other regions with lower reptile diversity (Tolley *et al.* 2016). This is also reflected by widespread data gaps in online data repositories, such as the Global Biodiversity Information Facility (GBIF) (Yesson *et al.* 2007). For example, Tolley *et al.* (2016) show that distribution data for reptile species from continental Africa represents less than 5% of available global reptile distribution records on GBIF, and they identified data accessibility and survey coverage as some of the major constraining factors associated with the current knowledge-gaps.

Extinction risk assessment of species from poorly surveyed regions may be underestimated or taxonomically biased when they are based on datasets from globally available data repositories (Yesson *et al.* 2007; Tolley *et al.* 2016). Therefore, alternative data-driven approaches such as species distribution modelling (SDM) has been proposed as a possible alternative for obtaining robust species distribution data from regions underrepresented by surveys and accessible biodiversity data (Tolley *et al.* 2016).

Even for regions within Africa that are relatively well-resourced, such as South Africa, reptile distribution data seems to largely reflect collecting effort because the majority of distribution records are mainly clustered around large metropolitan areas and major highways (Tolley *et al.* 2016). Despite collecting bias, South Africa's reptile fauna is

comparatively well-sampled compared to other African countries and reptile extinction rates tend to be lower than global averages (Böhm *et al.* 2013; Tolley *et al.* 2016; 2019). Although the majority of reptile species in South Africa are considered 'well protected', some of these threatened species have declining populations (Tolley *et al.* 2019). This may be because reptiles have traditionally not been the target of conservation interventions, so they remain under pressure and face extinction risk.

Only about half of the reptile species in mainland Africa have formal IUCN conservation assessments (Tolley *et al.* 2016). The number of unassessed species is likely to increase given the rapid rate at which new reptile species are being discovered and described, especially from previously inaccessible (and therefore poorly surveyed) African regions (Böhm *et al.* 2013; Tolley *et al.* 2016; 2019). Consequently, the seemingly unabating increase in African reptile species identification is likely to exacerbate the current knowledge-gap related to fundamental species information, ecological requirements, and distribution data (Tolley *et al.* 2016). All are essential for informing conservation assessments (Böhm *et al.* 2013; Tolley *et al.* 2016; 2019). African reptile species are believed to be most threatened by habitat transformation due to unsustainable agricultural land-use practices (Tolley *et al.* 2016; 2019). However, Tolley *et al.* (2019) suggested that the lack of information regarding these threats, coupled with the projected increase in human population density in Africa, is likely to elevate the current extinction risk for African reptile species.

Despite these prospects, not all reptile species will be affected in the same way. Tolley *et al.* (2016) showed that extinction risk was biased towards habitat specialists and narrow-ranged endemic taxa, particularly in the Viperidae, Chamaeleonidae,

Amphisbaenidae, and Cordylidae families, many of which have been shown to contain evolutionarily distinct cryptic species (Kelly *et al.* 2011; Greenbaum *et al.* 2012; Florio *et al.* 2012; Stanley *et al.* 2016; Tolley *et al.* 2016).

Vipers (also known as adders) are particularly vulnerable to extinction because of their unique life-history traits (Maritz *et al.* 2016; Tolley *et al.* 2016). However, thorough ecological studies that focus on aspects related to species demographics are mostly biased towards the northern temperate regions, so Africa remains largely neglected (Maritz & Alexander 2012a; Maritz & Alexander 2012b). This is especially apparent in a South African context, where information on the drivers of distribution patterns and threats of dwarf adders (*Bitis* spp.) remains poorly understood at local population scales, even though the region contains a high diversity of species (Turner & Branch, 2014; Maritz *et al.* 2016; Tolley *et al.* 2016; Tolley *et al.* 2019). Several are known to have very restricted geographic ranges and face considerable extinction risks because of habitat loss (Turner & Branch 2014; Tolley *et al.* 2016; Tolley *et al.* 2019). Moreover, some dwarf adder species (e.g. *B. atropos*) consist of a number of undescribed cryptic taxa, which are expected to be described in the near future (Kelly *et al.* 2011; Barlow *et al*. 2019). New species of dwarf adders resulting from taxonomic splits are likely to have narrow distributions because species description date is generally negatively correlated to range size and, therefore, newly described snakes are likely to be range-restricted (Böhm *et al.* 2017; Meiri *et al.* 2018).

Despite the high diversity of dwarf adders in South Africa, studies into their population sizes, habitat preferences, dispersal abilities, home range estimates, and densities are generally lacking (Maritz & Alexander 2012a; Turner & Branch 2014). These

shortcomings hamper conservation efforts for most reptile species in South Africa, and Tolley *et al.* (2019) suggest that such information could improve prioritization of conservation efforts in the region. However, collecting field data to elucidate these attributes is a daunting task and depends on the intrinsic and extrinsic biological traits of species. In this regard, snakes are considered to be among the most difficult to study reptiles because of their cryptic colouration, limited activity patterns, and overall wariness that limits detection during field surveys that may be further confounded when species occur in complex terrain (Steen 2010; Durso *et al.* 2011; Hansen *et al.* 2017). These traits all apply to South African dwarf adder species, which also exhibit traits known to increase the vulnerability of snakes, and particularly vipers, to extinction (small body size, habitat specialist and ambush foraging mode) (Maritz *et al.* 2016; Böhm *et al.* 2017).

In order to account for the cryptic nature of these snakes, any study that plans to quantify population parameters of dwarf adders must account for imperfect detection through standardized approaches using repeated sampling (Mazerolle *et al*. 2007; Steen 2010). In this respect, the ecology of dwarf adders are poorly understood because only a single study by Maritz & Alexander (2012b) explicitly accounted for limited detection using a mark-recapture approach. They estimated demographic parameters for *Bitis schneideri,* an arid-adapted dwarf adder that occurs in coastal dune systems along the west coast of South Africa (Maritz & Alexander 2012b). Apart from this pioneering study, no other quantitative ecological studies that account for imperfect detection exist for other snake species in South Africa.

Life in the *"atroposphere"*

Berg adders (*Bitis atropos*) are terrestrial, diurnal viperids, beleaguered by taxonomic uncertainty (Haagner & Hurter 1988; Jacobsen 1989; Kelly *et al.* 2011; Turner & Branch 2014). They are currently listed as “Least Concern” and are widely distributed across the eastern and southern parts of the Great Escarpment as well as the Cape Fold Mountains of southern Africa (Figure 1.1) where they occur in disjunct, presumably allopatric populations (Kelly *et al.* 2011; Turner & Branch 2014; Barlow *et al.* 2019). Across these mountain systems, six distinct evolutionary lineages of *B. atropos* are recognized (Kelly *et al.* 2011). Two of these lineages are restricted to Afromontane grasslands along the eastern escarpment of the Mpumalanga and Limpopo provinces, South Africa. These grasslands form part of South Africa’s grassland biome, which is threatened by habitat loss through fragmentation and transformation by agriculture, forestry and mining activities (Neke & Du Plessis 2004; Fourie *et al.* 2015). This region is also known for its biogeographic complexity and high local endemism, and consequently as an important area of speciation, especially for reptiles with low vagility like small-bodied adders (Clark *et al.* 2011; Kelly *et al*. 2011; Travers *et al.* 2014; Conradie *et al.* 2018).

Despite the current conservation status of the berg adder, *B. atropos,* being listed as “Least Concern”, Turner & Branch (2014) suggest that a revision of the group based on phylogenetic information would describe several new species, which will each require new conservation assessments. Preliminary phylogenetic analysis presented during a local conference confirms the existence of several species within the *B. atropos* species complex (Kelly *et al.* 2011). These results have more recently been highlighted by Barlow *et al.* (2019), who confirmed the likelihood of cryptic species within the *Bitis*

atropos species complex and suggested further research to clarify species-level splits. Sadly, the phylogenetic research by Kelly *et al.* (2011) has remained unpublished due to the recent passing of William R. Branch, who was the authority on this research topic.

One of the lineages of dwarf adder is limited to the Mpumalanga region of South Africa (Figure 1.1).

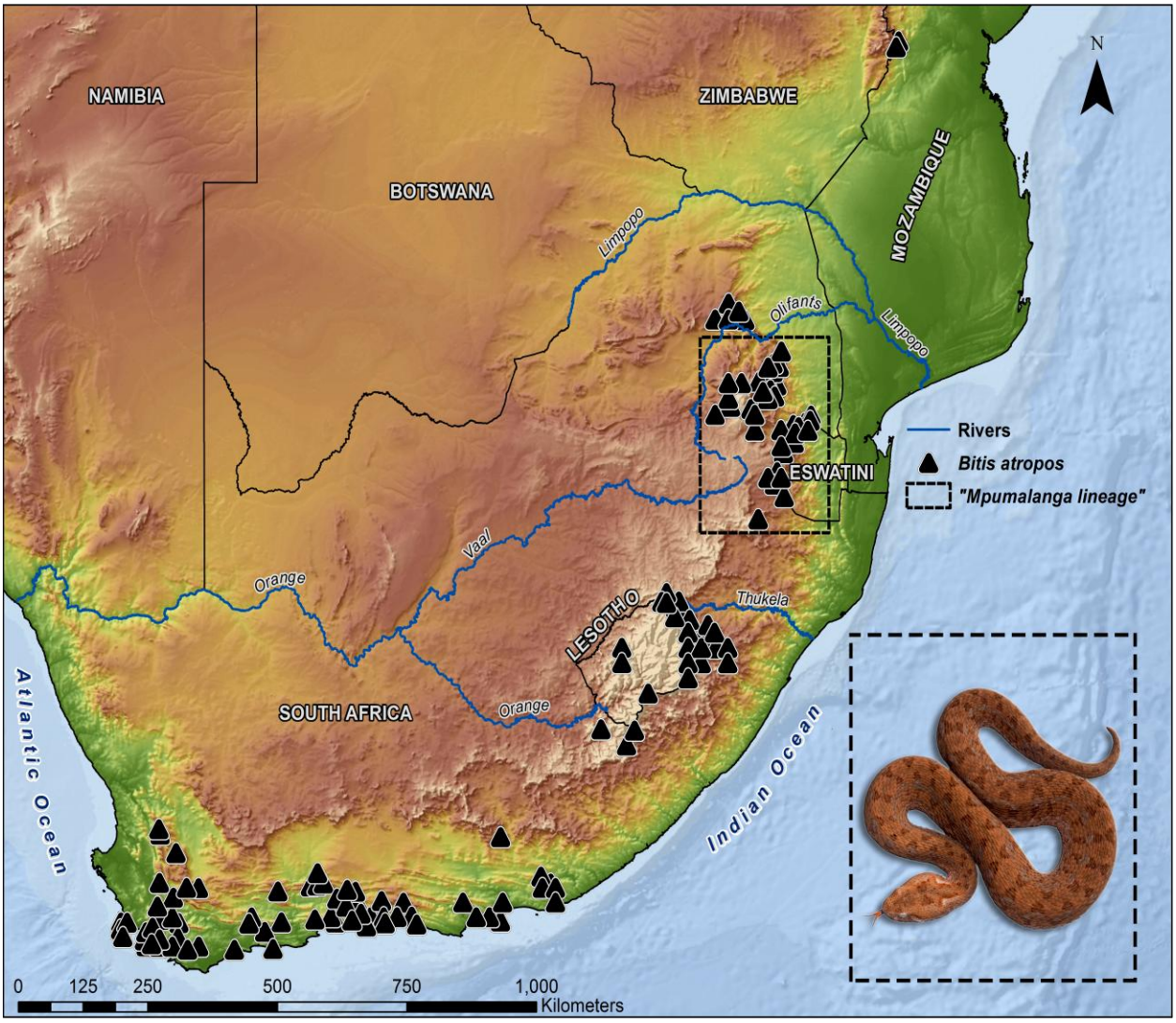

Figure 1.1 Geographic distribution of *Bitis atropos* across southern Africa. Map inset represents the known distribution of the Mpumalanga lineage (occurrence data: Animal Demography Unit, Mpumalanga Tourism and Parks Agency, and field surveys from this study).

This Mpumalanga lineage inhabits topographically heterogeneous areas in montane grassland between elevations of 1200 – 2200 m a.s.l. (Haagner & Hurter 1988; Jacobsen 1989). Within these areas, they are often found under or next to rocks or basking in grass tussocks (Jacobsen 1989; Branch 1998). Fitzsimons (1959) considered populations from the Belfast region of Mpumalanga as a subspecies - *B. a. unicolor* - on the basis of colour, scalation, and their apparent size difference from the nominate species. This subspecies was, however, subsumed into the *B. atropos* complex (Broadley 1983), and surveys by Haagner & Hurter (1988) alluded to *B. a. unicolor* being a local colour variation owing to its previously unknown distribution further south along the escarpment.

Berg adders are habitat specialists and generalist predators that feed on a variety of lizards, rodents, and amphibians, particularly rain frogs of the genus *Breviceps* (Branch 1998; Broadley & Blaylock 2013). Females are viviparous and give birth from early to late summer (Haagner & Hurter 1988; Jacobsen 1989). Litter sizes vary from 5-12 neonates with total lengths between 94.5 - 124.9 mm (Haagner & Hurter 1988). Adults seldom attain lengths larger (TL) than ~400 mm snout-vent length (SVL), however larger specimens have been observed (Jacobsen 1989; Branch 1998; Marais 2004).

The ecological aspects related to berg adder geographic distribution and habitat preferences remain generally unstudied. A single study from more than three decades ago (Haagner & Hurter 1988) provided only brief notes related to elevation, litter size, neonate mass, size, and reproduction. However, this pioneering study was based on opportunistic records from unstructured field surveys aimed at filling distribution gaps along the Mpumalanga and Eswatini (formerly Swaziland) escarpment. These data

undoubtedly provides a useful contribution to understanding the general natural history of this berg adder population, but falls short of informing scale-related drivers of habitat preferences and geographic distributions.

In this study, my supervisors and I (which I refer to using the pronoun ‘we’ throughout this manuscript) consider the Mpumalanga lineage to be restricted largely to the administrative boundaries of the province because of the absence of distribution records between the Mpumalanga and Limpopo lineages (Figure 1.1). Despite the relatively shorter geographic distance between the Mpumalanga and Limpopo lineages, William R. Branch (during email correspondence prior to his passing) maintained that a disjunction exists between these two lineages that led to deep genetic divergences between them. However, the taxonomic status of the various *Bitis atropos* lineages will most likely depend on taxonomic changes applied to other dwarf *Bitis* species, notably the species from the *cornuta-inornata* species complex for which further sampling is needed to clarify species boundaries and the validity of its members (Barlow *et al.* 2019).

Nevertheless, species splits related to the *B. atropos* species complex will increase the current knowledge-gap for dwarf adder ecology and conservation in South Africa. Therefore, in this dissertation, we address this fundamental knowledge gap by focusing explicitly on elucidating the habitat preferences and conservation of the Mpumalanga lineage of *B. atropos* because it is poorly studied and might represent a novel species.

Adding a piece to the puzzle of snake conservation and ecology in South Africa

Work presented in this dissertation broadly aims to answer fundamental ecological questions related to a cryptic lineage of berg adder (*B. atropos*) from the Mpumalanga province, South Africa, but aims to be as widely applicable to reptile species in general. The results of this dissertation are represented as separate free-standing chapters that are intended as independent unpublished preprints for future publication.

In chapter 2 (**Using species distribution models for pre-emptive conservation assessments under taxonomic uncertainty**), my objective was to evaluate the utility of pre-emptive conservation assessments for species with ambiguous taxonomic status. I did this using species distribution modelling (SDM) to evaluate the conservation status of the Mpumalanga lineage of berg adder. My co-authors and I were particularly interested in:

- Incorporating uncertainty from the SDM approach (in terms of modelling extent and the delineation of range margins) when estimating geographic range size,
- Combining range size data with information on land-use change and protected area coverage to quantify threatening processes and conservation responses for this lineage,
- Integrating range size predictions, threats and responses to assess the extinction threat of the Mpumalanga lineage.

In chapter 3 (**Habitat occupancy of the cryptic berg adder, *Bitis atropos*, is related to topographic patterns of ambient energy**), I address habitat use by berg adders at the scale of a specific reserve. Specifically, my co-authors and I set out to:

- Account for imperfect detection by using an occupancy modelling framework to model habitat preferences,
- Identify possible abiotic drivers of habitat occupancy using topography-derived variables,
- Draw ecological inferences of habitat use by the Mpumalanga berg adder lineage based on the association between habitat occupancy and topographic characteristics of the landscape.

By studying both the range-wide distribution and reserve-scale habitat use of the Mpumalanga berg adder lineage, we piece together multi-scale information on these snakes to ultimately inform their conservation and management. These lines of information and brought together in Chapter 4, which provides a general synthesis and summary of the findings presented in this dissertation. This concluding chapter will discuss the findings of this study within the context of reptile conservation and, more specifically, snake conservation and ecology.

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CHAPTER 2: Using species distribution models for pre-emptive conservation assessments under taxonomic uncertainty

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Unpublished manuscript

"Essentially, all models are wrong, but some are useful."

- **George E. P. Box**

Abstract

Reptile diversity is increasing globally as new species are discovered, and existing species complexes are revised. Newly recognised species often have narrow geographic ranges, are poorly represented within protected areas, and are, therefore, more vulnerable to habitat loss. This implies that they will be assigned to a high threat category once they are assessed according to IUCN Red List criteria. Pre-emptive conservation assessments of unresolved species complexes could close the gap between the recognition of new species and the assessment of their threat status. Here, we use species distribution models (SDMs) as a tool for estimating geographic ranges for a pre-emptive conservation assessment. We modelled the distribution of a distinct

evolutionary lineage of a cryptic snake species, the berg adder (*Bitis atropos*), in South Africa, which currently has an ambiguous taxonomic status. Our modelling framework accounted for different sources of uncertainty (related to geographic background extent and techniques for delineating range margins) and found that more liberal approaches classified the species as “Vulnerable”, while conservative approaches classified it as “Endangered”. Results also showed that, although species’ range was adequately represented by current protected areas, intact habitat within the species’ range has declined by 9 – 12 % over the last two decades. Combining these sources of information suggests that this snake could be classified at least as “Vulnerable” if it is formally recognised as a distinct species. This demonstrates the value of a standardised approach to pre-empt conservation assessments and to narrow the assessment-gap for newly described reptile species.

Keywords: cryptic species; pre-emptive conservation assessment; reptile diversity; species distribution models (SDMs); uncertainty.

Introduction

Reptiles are the most diverse group of terrestrial vertebrates globally, with an estimated 10 970 species currently recognised (Roll *et al.* 2017; Carranza *et al.* 2018; Uetz *et al.* 2019). Despite comprising a third of known terrestrial vertebrates (Roll *et al*. 2017), reptiles remain poorly studied, and knowledge of their extinction risk lags behind those of other terrestrial vertebrate groups. Furthermore, the number of newly described reptile species is continuously growing as existing species complexes are being split due partly to advances in molecular genetic techniques (Meiri 2016; Meiri & Chapple

2016). This contributes to the description of approximately 200 new reptile species each year (Meiri & Chapple 2016), of which some are likely to be either rare or range-restricted and therefore may require urgent conservation interventions (Vargas-Ramírez *et al.* 2016).

As is also the case for other taxonomic groups, reptiles are being threatened by habitat loss and degradation, invasive species, climate change and pollution. Despite this, detailed knowledge of reptiles' global extinction risk is limited to a single study, which at that time represented only 16% (currently 13.7%) of extant reptile species (Böhm *et al.* 2013). This means that reptiles are inadequately covered by conservation assessments and are regularly overlooked during conservation interventions. For instance, reptiles are poorly represented in protected areas compared to birds and mammals (Meiri & Chapple 2016; Roll *et al.* 2017; Carranza *et al.* 2018). Therefore, reptile conservation assessments need to overcome the dual obstacles caused by the proliferation of new species descriptions and being chronically under-researched.

Due to being poorly studied, the conservation statuses of only 45% of currently described reptile species have been assessed by the International Union for Conservation of Nature (IUCN) (Tingley *et al.* 2016). The most commonly used assessment metric applied in IUCN Red List (i.e. conservation) assessments is restricted range size (Criterion B1), which is measured as the species' extent of occurrence (EOO) in km^2 (Gaston & Fuller 2009; Meiri & Chapple 2016). EOO is favoured for conservation assessments because it functions as a proxy for extinction risk and is relatively easy to quantify for species with well-known geographic ranges (Syfert *et al.* 2014). For a species to occupy a threatened category under Criterion B1

(Vulnerable [VU], Endangered [EN], Critically Endangered [CR]) it has to adhere not only to the range restricted thresholds (VU < 20,000 km^2, EN < 5000 km^2, CR < 100 km^2; IUCN 2017) set-out by the guidelines of the IUCN, but also has to satisfy other sub-criteria related to the extent and quality of species habitat (Ramesh *et al.* 2017). Despite the relative ease with which EOO can be calculated, for a taxonomic group such as reptiles, whose geographic distributions are comparatively poorly known, EOO might still be difficult to calculate due to limited data. The IUCN under such circumstances, therefore, recommends that either the known, inferred, or projected geographic ranges of species can be used to estimate EOO (Ahmadi *et al.* 2019), which subsequently provides opportunities for using alternative data-driven approaches to quantify range size.

One approach of making the most of sparse data is using species distribution models (SDMs) (Guisan *et al.* 2017). SDMs are proven to be effective in conservation assessments and are, therefore, a widely used surrogate method to estimate geographic range size (EOO), as well as trends in threatening processes and the amount of suitable habitat under formal protection (Anderson & Martínez-Meyer 2004; Thorn *et al*. 2009; Cassini 2011). Furthermore, these models are recognised to perform well even when biological knowledge and distribution data is limited (Pena *et al.* 2014), which is often the case for cryptic species with ambiguous taxonomic status (Pearson *et al.* 2007).

Determining the geographic range of understudied data-poor species, even when using efficient data-driven techniques such as SDMs, remains a complex challenge due to the uncertainty inherent to model-based predictions. One of the most prominent contributors

to predictive uncertainty is related to the spatial scale at which SDMs are implemented (Guisan & Thuiller 2005; Barve *et al.* 2011). Inappropriately defined components of spatial scale such as the extent of the study area (i.e. background data) can lead to a mismatch between the scale at which models are fit and the scale at which ecological processes occur (Guisan & Thuiller 2005; Acevedo *et al.* 2012). For example, increasing the study extent beyond dispersal capabilities of the study species and including areas known to be unsuitable for the species increases the predictive power of the resultant model (according to evaluation statistics), without providing additional information. Therefore, when choosing the extent of background data, the specific purpose of the model needs to be considered carefully. This is particularly important when the intended use of models is for conservation purposes (El-Gabbas & Dormann 2018).

Because the implementation of conservation interventions often depend on administrative boundaries, these boundaries regularly inform the choice of modelling background extent (Guisan & Thuiller 2005; Raes 2012; El-Gabbas & Dormann 2018). However, these boundaries may be completely unrelated to the habitat requirements of the species being modelled. An alternative approach is identifying the background extent based on a pre-defined buffer around known species occurrences. However, this approach can be invalidated by incomplete survey records. A third way of selecting the extent of background is using large-scale geophysical features that are known to be linked to the species' ecology. This approach does, however, ignore the possibility that dispersal limitation prevents species from expanding their ranges across the entire extent of the geophysical feature. Since each of these approaches has its own strengths

and weaknesses, choosing between them can be an arbitrary decision that is a source of uncertainty in the eventual model prediction.

Another inherent source of uncertainty in SDM is introduced because they reduce continuous species distributions to binary range maps in order to estimate the EOO (Suárez-Seoane *et al.* 2018). Since range boundaries are fundamentally fuzzy because individual organisms can move in space, multiple ways to delineate range boundaries from SDM outputs have been developed (Peck 2009; Bean *et al.* 2012; Vale *et al.* 2014). Some of these are liberal and prone to overestimating range size, while others are conservative and susceptible to underestimating range size. Therefore, a robust pre-emptive conservation assessment should consider the sensitivity of different range delineation methods explicitly.

In this study, we demonstrate how sources of uncertainty associated with background extent and delineating range margins can be considered during the SDM process. We do this for a distinct lineage of berg adder (*Bitis atropos*), a small-bodied diurnal viperid, with an ambiguous taxonomic status (Kelly *et al.* 2011; Turner & Branch 2014). The species is currently listed by the IUCN as “Least Concern” due to its wide, although disjunct, distribution throughout southern Africa where it occurs mainly in montane habitats (Kelly *et al.* 2011; Turner & Branch 2014). However, the current species (*Bitis atropos sensu lato*) comprises of six distinct evolutionary lineages, of which some, if not all, merit species status recognition (Kelly *et al.* 2011). Owing to this knowledge, Turner & Branch (2014) recommended that pending the outcome of a formal taxonomic revision, the threatened status of all newly recognised species should be assessed to identify if any conservation interventions are required. One of these lineages –

previously recognised as a subspecies *B. a. unicolor* – is likely to represent an undescribed candidate species based on morphological and phylogenetic studies (Fitzsimons 1959; Haagner & Hurter 1988; Jacobsen 1989; Kelly *et al.* 2011). However, little is known about the geographic distribution, protection and threat levels of this lineage (Haagner & Hurter 1988).

The overall aim of this study was to use SDMs to model the geographic distribution of a distinct evolutionary lineage of berg adder (*B. atropos*) in South Africa. Specifically, we first set out to estimate its geographic range size using SDMs, while acknowledging uncertainty from our choice of background extent and methods for delineating range margins. We then quantified historical habitat transformation within the predicted geographic range to estimate the severity of threatening processes. Lastly, we evaluated the current protection level of suitable habitat areas. By combining these data on spatial extent, threat and protection level, we assessed the conservation status for this cryptic species and illustrated the value of a pre-emptive approach to conservation assessment.

Materials and methods

Species occurrence records

Occurrence records for *B. atropos* were obtained from four sources: (1) from a structured field survey at the Buffelskloof Private Nature Reserve (BKPNR) between 2016 to 2017; (2) random unstructured field surveys across the known distribution of Mpumalanga escarpment between 2012 to 2017; (3) from digitized museum records (Animal Demography Unit 2014); and (4) from records provided by the Mpumalanga

Tourism and Parks Agency (MTPA), the local conservation authority. This initial dataset consisted of 483 records; however, many of these records were highly clustered around a few localities or had high spatial uncertainty. For this reason, we used both temporal and spatial filtering to reduce the number of occurrences. Only records after the year 2000 were retained because these all had reliable georeferenced coordinates. Similarly, when points were clustered within ~1 km, we randomly selected only one of these records using SDMtoolbox (Brown 2014) because this minimized the spatial dependency among records to improve model performance (Phillips *et al.* 2009; Boria *et al.* 2014). Our final dataset, after temporal and spatial filtering included 33 geographically unique occurrence records (*n* = 4 structured field surveys; *n* = 21 unstructured field surveys; *n* = 6 museum records; *n* = 2 MTPA records). Despite this substantial reduction in the number of occurrence records post-filtering, the dataset still contained occurrences representative of the lineages' known geographic range and also remains sufficiently large to obtain reliable and robust estimates of geographic range size from the statistical modelling approach considered in this study (Elith *et al*. 2006; Pearson *et al*. 2007; Platts *et al*. 2014).

Environmental predictor variables

We chose predictor variables known to influence habitat structure, resource availability and considered to be important limiting factors of reptile distributions (Guisan & Thuiller 2005; Lyet *et al.* 2013; Lewin *et al.* 2016; Mizsei *et al.* 2016). We initially considered elevation (DEM), temperature seasonality (BIO 4), minimum temperature of the coldest month (BIO 6), precipitation of the coldest month (BIO 13), precipitation seasonality (BIO 15), and a topographic position index (TPI) as optimal modelling predictors based

on the ecology of our study species. However, we subsequently excluded elevation (DEM) after screening variables for multicollinearity using Pearson's correlation coefficient implemented by the 'corrplot' (Wei *et al.* 2017) package in R version 3.4.3 (R Core Team 2017) (Supporting information: Figure S2.1, p.55) because it was strongly correlated (r = -0.94) with precipitation of the coldest month (BIO 6). Climatic variables are generally considered stronger predictors than distal predictors such as elevation which could act as a proxy for other unknown underlying environmental variables (Bradie & Leung 2017; Guisan *et al.* 2017). All bioclimatic variables originated from the WorldClim database (Hijmans *et al.* 2005, available online at http://www.worldclim.org) and elevation data were obtained from the Shuttle Radar Topography Mission (SRTM) (Jarvis *et al.* 2008). TPI was derived from the SRTM elevation layer using Land Facet Corridor Designer (Jenness *et al.* 2013) in ArcGIS 10.2.1 (ESRI 2012). All variables used for modelling were resampled to a resolution of 30 arc-seconds (~1km).

To reduce uncertainty of model-based geographic range size predictions, we restricted background selection to known areas of this lineages' distribution using three different extents. This was done to ensure that our background extents accounted for environmental heterogeneity associated with the lineages' known distribution and also to reduce the possibility of truncating important range limiting ecological gradients. Each of these extents differed inherently in their assumptions, advantages and limitations for conservation planning and implementation (Table 2.1).

Table 2.1 Description of background extents used in MaxEnt to predict the geographic distribution of *B. atropos.*

Scale	Description	Advantage(s)	Limitation(s)
Administrative boundaries	Background data restricted to the geopolitical boundaries of Mpumalanga Province, South Africa and neighbouring Eswatini	Reflects the area where conservation interventions are planned and implemented	Not biologically relevant Fails to capture complete environmental gradients Includes climatically suitable but unavailable habitat
Habitat requirements	Background data delineated according to a map of mountainous escarpment (determined by a regional scale topographic position index)	Ecological realism linked to general species requirements	Assumes that the species is at equilibrium with the environment and thus has perfect dispersal
Species records	Background data restricted to the known occurrence records surrounded by a rectangular minimum convex polygon fitted to the most extreme records in all four cardinal directions and buffered by 50km	Based on reliable records of the known distribution Accounts for limited dispersal Does not include large unsuitable or unavailable habitat	Susceptible to sampling bias

Our approach for selecting different background extents was based on and delimited according to the: (1) administrative boundaries of the Mpumalanga Province in South Africa and the neighbouring country of Eswatini (formerly known as Swaziland), (2) biophysical habitat requirements of the species and (3) known species records. These background extents, however, differ from one another not only in the amount of unsuitable habitat they include, but also the area of suitable habitat unavailable to the species due to assumed dispersal constraints.

Species distribution models

We used MaxEnt version 3.4.1 (Phillips *et al.* 2006; Phillips & Dudík 2008; Phillips *et al.* 2017) to model the distribution of *B. atropos*. MaxEnt is based on the principle of maximum entropy and one of the most robust and widely used presence-only SDM methods, especially for small sample sizes and few predictor variables (Elith *et al.* 2006; Pearson *et al.* 2007; Platts *et al.* 2014). The resulting model output is a continuous probability of environmental similarity or habitat suitability ranging from zero (least suitable) to one (most suitable) (Anderson & Gonzalez 2011; Merow *et al.* 2013).

We restricted MaxEnt to fit models using only linear and quadratic features types. These were selected because of their ability to produce simple, yet robust models, not prone to over-fitting when sample sizes are low (Anderson & Gonzalez 2011; Syfert *et al.* 2014). MaxEnt's default output was retained, and models were run using with the regularisation multiplier set to 1 and the maximum iterations set to 500. The occurrence dataset was partitioned into 70% for model calibration and the remaining 30% for model validation.

All models were replicated 100 times using the bootstrap (sampling with replacement) replicated run type and subsequently averaged to evaluate model performance.

Model performance was assessed using the threshold-independent area under the curve (AUC) of the receiver operating characteristic (ROC) for both training and test data. AUC compares rates of correctly predicted presences with randomly selected background points across the modelling extent and values range between 0.5 (no better than random) and 1 (perfect fit). Models with AUC values > 0.8 are considered to have reasonably good fits (Swets 1988; Araújo *et al.* 2005). However, AUC has received criticism primarily because it is influenced by background extent (Lobo *et al.* 2008). For this reason, we also considered the threshold-dependent true skill statistic (TSS), which takes both omission (false negative) and commission (false positive) errors into account (Allouche *et al.* 2006; Barbosa *et al.* 2017). TSS values range between -1 to +1, where higher values (TSS > 0.4) represent better fits and negative values are considered no better than random (Allouche *et al.* 2006).

Because conservation assessments require an estimate of a species' EOO, we transformed the continuous MaxEnt model outputs into binary maps. This was done by applying different thresholds calculated from the ROC plot to classify models into areas of 'suitable' and 'unsuitable' habitat (Hernandez *et al.* 2008; Bean *et al.* 2012). Although the choice of threshold selection is somewhat arbitrary (Liu *et al.* 2005), we chose three thresholds known to perform well but which differ in how they optimise inclusion rates of known occurrences based on the ROC plot (Pearson *et al.* 2007; Cao *et al.* 2013). These thresholds were: minimum training presence (MTP), which we considered as a liberal threshold due to it maintaining the smallest predicted area including all the

training data; equal training sensitivity and specificity (EquSS), which weighs omission and commission errors equally; and maximum training sensitivity plus specificity (MaxSS), which minimises omission and commission errors by maximising the sum of sensitivity and specificity while optimising the amount of training data included. We considered both EquSS and MaxSS as conservative thresholds for range size estimation due to their assumptions of inclusion of training data relative to the background extent. These thresholds were applied to each of our three background extents to produce nine distribution models, which were used to quantify EOO and compare to IUCN Red List criteria for different threat levels (VU < 20,000 km^2, EN < 5000 km^2, CR < 100 km^2: IUCN 2017). Lastly, we combined predictions from all models to create an ensemble model of individual model overlap using the r.series function of GRASS (www.grass.osgeo.org) in QGIS 3.2 (www.qgis.org). All other spatial analysis was done in ArcGIS 10.2.1 (ESRI 2012).

Estimating threat and protection levels

We quantified the habitat intactness (as a proxy for trends in threatening processes) and the representation of the species in current protected areas (as a proxy for conservation interventions) based on the estimated geographic range sizes obtained from SDM outputs. Two land cover datasets (1990 and 2014), obtained from the Department of Environmental Affairs (DEA 2018) of South Africa (https://egis.environment.gov.za/) were overlaid with the nine predicted range models to represent the parts of the species' range that have been transformed due to anthropogenic activities. Land cover classes were reclassified into two states – intact or transformed – based on observed and reported habitat requirements of the species

(Haagner & Hurter 1988) (Supporting information: Methods S2.1, p.55; Table S2.1, p.56).

We then investigated if there was a loss of habitat between 1990 and 2014 within the predicted geographic range estimates. The land cover datasets only covered areas from South Africa and consequently the marginal distribution in Eswatini could not be quantified for this analysis. We, however, expected similar trends in threatening processes to affect habitat intactness, due to similar environmental conditions associated with the marginal distribution of the escarpment into Eswatini.

Lastly, we quantified the extent of the geographic range within formally protected areas (PAs) by intersecting range predictions with a merged PA dataset from the DEA and World Database on Protected Areas (WDPA) (https://www.protectedplanet.net/). We considered geographic range estimates as "adequately protected" when at least 12% of the predicted geographic range intersected with current PAs, because this threshold has been used by similar evaluation of reptile protection (Vasconcelos *et al.* 2012; Carranza *et al.* 2018). We performed all geoprocessing analysis, for both land cover and protected areas, in ArcGIS 10.2.1 (ESRI 2012).

Results

The predictive power of the nine SDMs was high (AUC_{test} and $AUC_{train} \geq 0.93$; TSS ≥ 0.59; Supporting information: Table S2.2, p.61) and their range outputs overlapped closely (Figure 2.1). The models provided a good representation of the known, observed distribution and indicated that suitable habitat is largely restricted to regions of the eastern escarpment of South Africa. Although the different models produced similar

outputs, some general trends emerged. The liberal modelling threshold (MTP) always predicted the most extensive range but tended to overestimate western parts of the distribution. This was followed by more strict conservative thresholds EquSS and MaxSS, predicting the smallest ranges. Models based on background data limited to the known habitat requirements of the species predicted the smallest distribution ranges.

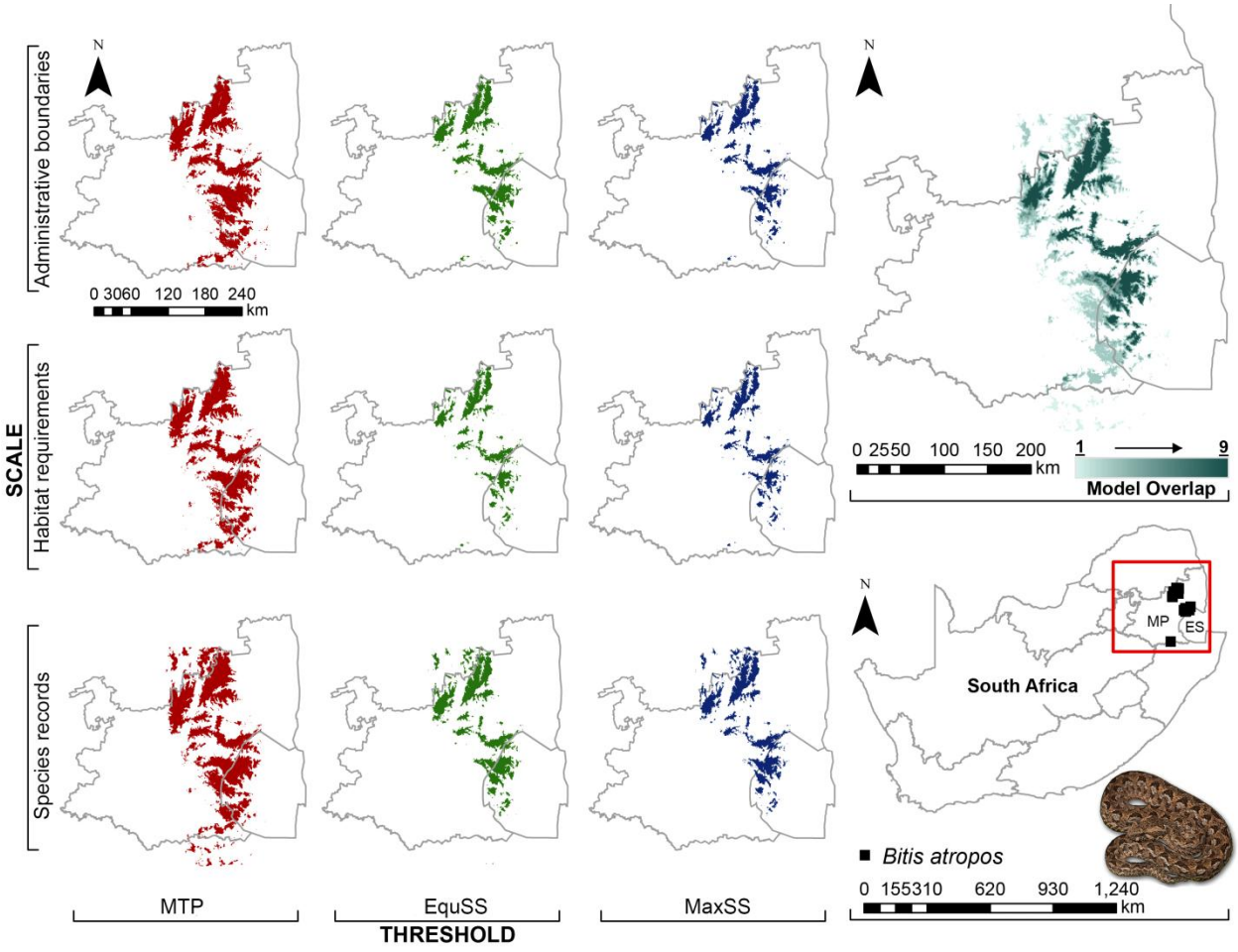

Figure 2.1 Predicted geographic distribution of *B. atropos* based on binary transformed MaxEnt model outputs. Model outputs are arranged based on the background extents (rows) and modelling thresholds (columns), and are combined in a single ensemble model of overlap (top right) with the relative position of the study region in South Africa (bottom right). Squares represent occurrence records used in this study.

When compared to the EOO thresholds for the different threat levels, seven out of nine range models classified the berg adder as “Vulnerable” (Figure 2.2). The remaining two models – based conservative thresholds and on background data constrained to the expected habitat preference of the berg adder – classified this species as “Endangered” (Figure 2.2). Our habitat analysis further revealed that approximately half of the habitat within the predicted range of the berg adder has already been transformed (Table 2.2).

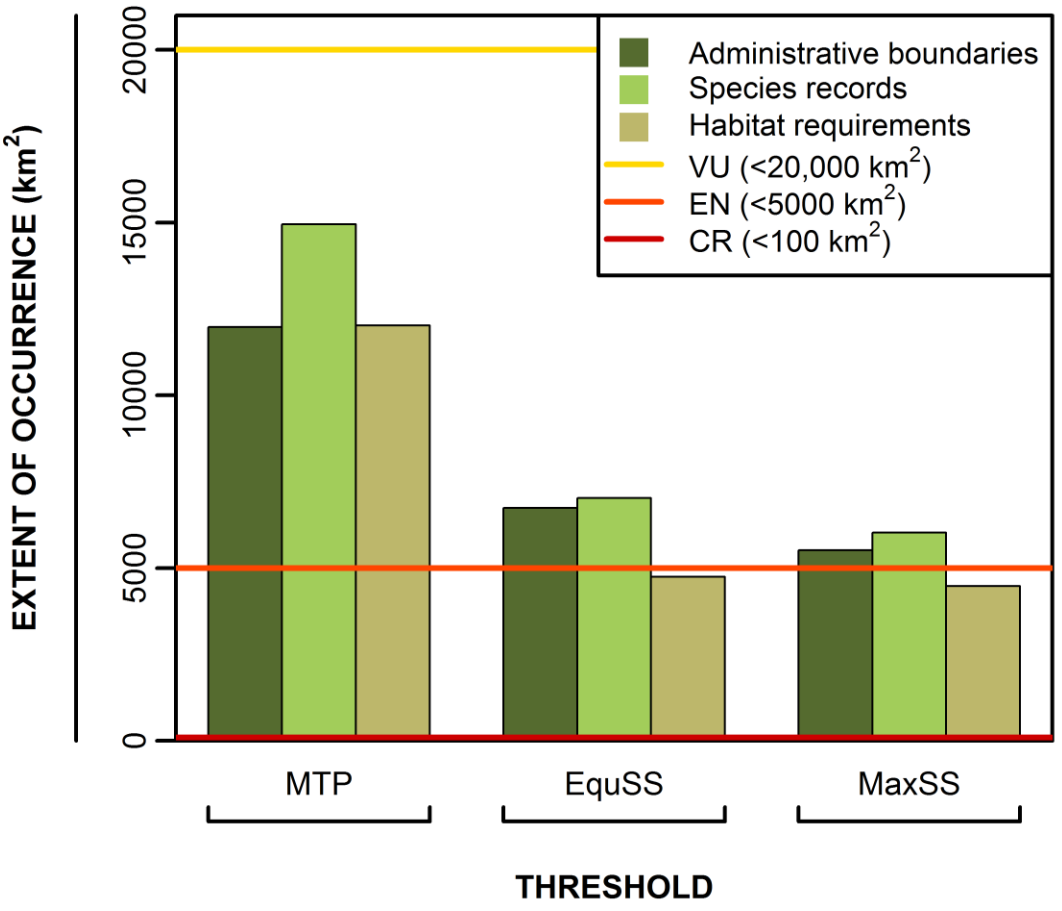

Figure 2.2 Estimates of range size from MaxEnt model predictions. Horizontal lines indicate different threatened categories according to IUCN geographic range size thresholds (Criterion B1).

Moreover, in the 24 years between 1990 and 2014, the amount of intact habitat within the species' range has declined by between 9.0 and 12.1%, depending on which model is used for the species EOO. The increasing loss of habitat within the berg adders geographic range further supports classifying this cryptic species as "Vulnerable" and perhaps even "Endangered".

Table 2.2 Estimates of habitat intactness and transformation between 1990 and 2014.

		Area of intact habitat in km^2 (values in brackets = %)		Percent intact habitat change
Scale	Threshold	1990	2014	1990 – 2014
Administrative boundaries	MTP	3998.6 (53.7)	3568.6 (51.1)	-10.7
	EquSS	2177.4 (55.3)	1974.0 (53.6)	- 9.3
	MaxSS	1767.3 (55.0)	1607.1 (53.5)	- 9.0
Habitat requirements	MTP	3993.8 (53.0)	3575.9 (50.5)	-10.4
	EquSS	1554.6 (55.1)	1416.6 (53.9)	- 8.8
	MaxSS	1483.9 (55.3)	1352.6 (54.1)	- 8.8
Species records	MTP	5308.6 (56.2)	4664.4 (53.0)	-12.1
	EquSS	2353.8 (59.1)	2128.9 (57.3)	- 9.5
	MaxSS	2049.8 (60.6)	1850.8 (58.8)	- 9.7

The number of protected areas predicted to contain suitable habitat was similar between background extents using the same thresholds. However, the proportion of predicted habitat within PAs varied between 9.9 and 23.7%. The EquSS and MaxSS thresholds always predicted proportionally more suitable habitat in protected areas when compared with the MTP threshold for all background extents. The majority of models (8 out of 9) predicted that the geographic range was more protected than the 12% threshold for being adequately protected (Table 2.3).

Table 2.3 The predicted geographic range of berg adder habitat in protected areas.

Scale	Threshold	Area of predicted geographic range in protected areas (km^2)	Number of protected areas predicted to contain suitable habitat	Percentage predicted suitable habitat in protected areas
Administrative boundaries	MTP	1472.0	65	12.2
	EquSS	1160.3	50	17.2
	MaxSS	1056.5	48	19.1
Habitat requirements	MTP	1493.8	58	9.9
	EquSS	969.7	46	13.7
	MaxSS	952.3	45	15.8
Species records	MTP	1570.2	64	13.0
	EquSS	1116.2	48	23.5
	MaxSS	1064.6	47	23.7

Discussion

Reptiles are the most understudied and most poorly known taxonomic group of terrestrial vertebrates (Roll *et al.* 2017; Carranza *et al.* 2018). However, the rapid rate at which new species are discovered described and redescribed from existing species complexes coupled by data gaps limits estimates of their extinction risk (Meiri 2016; Meiri & Chapple 2016). Therefore, alternative approaches to quantifying geographic range size, which account for data limitations could greatly narrow the current assessment gap of reptiles globally, especially under situations of taxonomic uncertainty.

In this study, we used SDMs as part of a pre-emptive conservation assessment for a lineage within the unresolved species complex of *B. atropos*. Our approach explicitly considered the uncertainty associated with the choice of background extent and thresholds for delineating range boundaries under an SDM framework. Based on predicted range size estimates, threat status was affected more by the choice of the delineation threshold than by the choice of the background extent. Despite this uncertainty, model outputs suggested that, should the Mpumalanga lineage of *B. atropos* be classified as a distinct species, it may merit uplisting from its current threat status of "Least Concern" to at least "Vulnerable" based on the IUCN's Red List criteria of range restrictedness (Criterion B1). This listing is further supported by increased habitat loss within this lineage's geographic range.

Range-based conservation assessment

The most commonly used criterion for assigning species to threat categories is geographic range size (Gaston & Fuller 2009). SDMs offers a promising way to define species ranges using limited data. The majority of our models assigned the Mpumalanga lineage of *B. atropos* to a category of "Vulnerable" based on restricted range size alone. However, some of our model outputs even classified this lineage as "Endangered" when the background extent was based on broad habitat requirements and the range margins were delineated according to equal or maximum sensitivity and specificity thresholds. This illustrates that the uncertainty inherent in the SDM process could be the determining factor when assessing extinction risk and highlights the importance of making the sources of uncertainty explicit.

Consistent with previous studies (Nenzén & Araújo 2011; Liu *et al.* 2013), we found that the choice of the threshold for delineating range margins tended to be the greatest source of uncertainty when estimating range size. Conservative thresholds always predicted smaller ranges than liberal thresholds, regardless of the background extent used to train the models. The choice of delineation thresholds cannot be resolved by improved data or more nuanced model validation because range margins may be fundamentally indeterminate. Non-equilibrial colonisation, extinction and habitat variability at range margins mean that species distributions cannot be defined as a single consistent boundary through time (Holt & Keitt 2000; Holt *et al.* 2005). Therefore, we maintain that the most robust approach to modelling species' ranges for conservation assessment is one that explores how sensitive the extinction threat classification is to the choice of different thresholds.

Selecting appropriate background extents when modelling species distributions is a well-known and often criticised issue in distribution ecology (Guisan & Thuiller 2005; Barve *et al.* 2011; Acevedo *et al.* 2012). This is partly because model fit and the choice of threshold both depend on the background area used for model calibration (Guisan & Thuiller 2005; Barve *et al.* 2011; El-Gabbas & Dormann 2018). Therefore, background selection should, as far as possible, be informed by available species data and areas where the species is reasonably expected to occur (Raes 2012). However, this remains difficult when the biological requirements of species are poorly understood due to limited data, as is the case for the majority of newly described species.

Our approach of background selection considered this by accounting for *a priori* assumptions relating to species' intrinsic biological requirements (i.e., known habitat

preferences), regions of conservation planning and implementation and areas that may be suitable but that are not occupied (i.e., due to dispersal constraints), all while acknowledging the advantages and limitations of each background extent. Despite the shortcomings of inappropriately delineated background extents, our models varied only slightly in their performance. This indicates that the background extents we managed to capture sufficient environmental variability to produce robust estimations of geographic range size.

Estimating threatening processes

Vipers are recognised globally as a group of snakes that are severely threatened and impacted by extinction due to ongoing loss, fragmentation, and degradation of suitable habitat (Maritz *et al.* 2016). Unsurprisingly, these threats are also the primary factors driving the extinction risk of African viper species (Tolley *et al.* 2016; 2019). Our results suggest that this also holds true for the Mpumalanga berg adder lineage, which has experienced widespread habitat transformation within its potential range. Similar patterns of habitat-loss threatened other reptiles within southern Africa (Parusnath *et al.* 2017; Tolley *et al.* 2019).

Despite considerable habitat loss prior to 1990, our results showed that habitat loss due to land-use change has continued unabated within the potential geographic range of the Mpumalanga berg adder. Specifically, ~10% of habitat within this snake's range has been transformed between 1990 and 2014. Therefore, our findings corroborate those of Böhm *et al.* (2013) who emphasised how ongoing habitat loss can increase extinction risk, especially for small-bodied and range-restricted snake species with specialised

habitat requirements, such as berg adders, might be more vulnerable to extinction (Böhm *et al.* 2017).

Habitat in protected areas

Globally, an important impediment to reptile conservation is the inadequacy of the global protected areas network to sufficiently capture reptiles' geographic ranges. On average, only 3.5% of their geographic ranges intersect with the current global protected areas network, a figure that is almost 50% less than that of other taxonomic groups (i.e., birds and mammals; Roll *et al.* 2017). The poor representation of reptiles within the current global protected areas network alludes to a taxon-specific bias in protected area designation, which is unsurprising, considering that reptiles represent the most understudied and poorly known group of terrestrial vertebrates (Roll *et al.* 2017; Tolley *et al.* 2019). In our study, however, the Mpumalanga berg adder would be considered well-protected based on the minimum threshold (12%) of predicted suitable habitat existing within protected areas (Vasconcelos *et al.* 2012; Carranza *et al.* 2018).

Although our results indicate that berg adders are adequately represented within the current protected areas network, this does not necessarily guarantee their persistence. This is because PAs rarely have management plans for non-charismatic species such as snakes (Roll *et al.* 2017), which is worrying, considering that snakes are suffering widespread population declines (Gibbons *et al.* 2000; Reading *et al.* 2010). Therefore, while our predicted protection status for berg adders in Mpumalanga is promising, follow-up monitoring could confirm PA effectiveness (Sewell *et al.* 2012).

Conclusion

This study demonstrated a promising approach for assessing the conservation status of unnamed cryptic taxa from existing species complexes prior to formal descriptions. This can narrow the gap between the current rates at which new reptile species are described and the rate at which formal conservation assessments can keep up. However, for pre-emptive conservation assessments to be effective, they need to be explicit about uncertainty inherent to the modelling approach. Moreover, our approach of using SDMs to evaluate threat status (and other approaches based on EOO) assumes that population density is uniformly distributed and constant across the estimated geographic range. This is unlikely to be the case in reality, so broad-scale SDM estimates should ideally be supplemented by smaller-scale estimates of habitat use. Nevertheless, pre-emptive conservation assessments based on SDMs provide an important stepping stone to overcome the obstacles in reptile conservation, while accounting for sparse data and uncertainty. This demonstrates the value of a standardised approach to pre-empt conservation assessments and to narrow the assessment-gap for newly described reptile species.

Acknowledgements

We thank the National Research Foundation (NRF) for providing financial support to Prof. N. Heideman (grant no. IFR150216114248) and for awarding A. Jordaan with an Innovation Scarce Skills Development Masters Scholarship. Permits to carry out this research were obtained from the Mpumalanga Tourism and Parks Agency (MTPA) under permit no. MPB. 5571/2, and ethical clearance was provided by the University of

the Free State's Animal Ethics Committee (clearance no. UFS-AED2016/0115). Dr. Mervyn (MTPA) Lotter and Dr. Hannes Botha (MTPA) are thanked for their willingness to share locality information.

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Supporting Information: Chapter 2

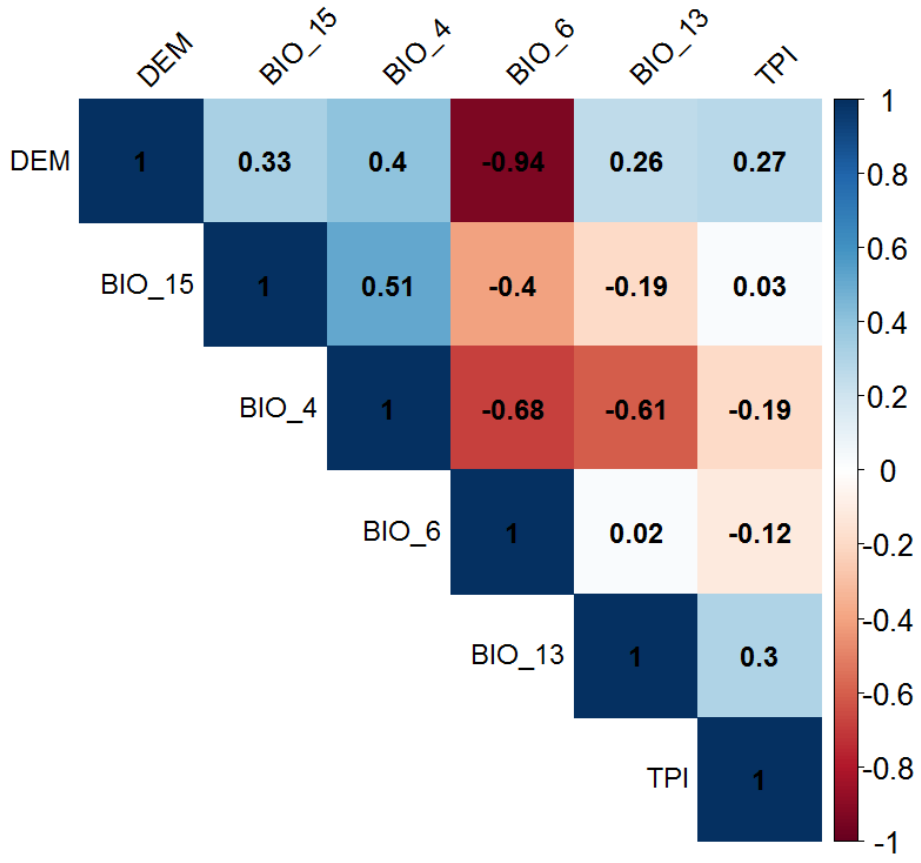

Figure S2.1 Pairwise comparisons among environmental predictors assessed using Pearson's correlation coefficient.

Methods S2.1

Land cover class selection

We considered the following land cover classes in our habitat analysis following the precautionary principle (IUCN 2017): 4 (low shrubland), 12 (wetlands) and 13 (grasslands). The area (in km²) of these classes were subsequently calculated and compared between two time steps (1990 and 2014; DEA 2018) to investigate habitat change. Although other natural habitat is available to the species, they have not been recorded in them. This could be due to unfavourable biotic interactions or fine-

scale microhabitat requirements. However, this is speculative, and we, therefore, decided to remain conservative and only considered habitat classes as suitable based on known and observed records of the species habitat requirements. Lastly, the rationale was that a decline in these habitat classes would directly influence the persistence and survival of the species.

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Table S2.1 Land cover class selection and area of intact habitat between 1990 and 2014 as predicted by MaxEnt for different background extents (a-i).

(a)

Administrative _MTP			
Land cover classes	**Intact/Transformed**	**Area_1990 (km^2)**	**Area_2014 (km^2)**
Low shrubland	Intact	57.5073	42.2604
Wetlands	Intact	183.2139	179.1027
Grasslands	Intact	3757.977	3347.2971
Plantations / Woodlots	Transformed	3126.0573	3056.3622
Cultivated commercial annual crops non-pivot	Transformed	123.597	124.8885
Cultivated commercial annual crops pivot	Transformed	1.4733	2.9115
Cultivated commercial permanent orchards	Transformed	3.3255	5.3073
Cultivated subsistence crops	Transformed	74.7828	77.1273
Settlements	Transformed	82.3068	89.8992
Mines	Transformed	4.1166	5.5521
Waterbodies	Transformed	5.8005	8.2305
Bare Ground	Transformed	9.1458	35.6967
Degraded	Transformed	6.4188	5.7483
Total area intact (km^2)		**3998.6982**	**3568.6602**
Total area transformed (km^2)		3437.0244	3411.7236
Total		7435.7226	6980.3838

Percentage intact	53.77686091	51.12412587

(b)

Administrative _EquSS			
Land cover classes	**Intact/Transformed**	**Area_1990 (km^2)**	**Area_2014 (km^2)**
Low shrubland	Intact	34.7967	29.9853
Wetlands	Intact	77.9742	76.7232
Grasslands	Intact	2064.7098	1867.3911
Plantations / Woodlots	Transformed	1632.033	1548.9675
Cultivated commercial annual crops non-pivot	Transformed	25.4007	28.6155
Cultivated commercial annual crops pivot	Transformed	1.1655	0.2385
Cultivated commercial permanent orchards	Transformed	0	1.7163
Cultivated subsistence crops	Transformed	43.6257	44.4321
Settlements	Transformed	45.1845	52.4934
Mines	Transformed	1.6011	0.5265
Waterbodies	Transformed	1.4076	3.3471
Bare Ground	Transformed	4.9329	24.2901
Degraded	Transformed	2.232	2.007
Total area intact (km^2)		**2177.4807**	**1974.0996**
Total area transformed (km^2)		1757.583	1706.634
Total		3935.0637	3680.7336
Percentage intact		55.33533549	53.63331918

(c)

Administrative _MaxSS			
Land cover classes	**Intact/Transformed**	**Area_1990 (km^2)**	**Area_2014 (km^2)**
Low shrubland	Intact	28.9737	25.7634
Wetlands	Intact	57.2949	56.3256
Grasslands	Intact	1681.1163	1525.0698
Plantations / Woodlots	Transformed	1357.9443	1276.8786
Cultivated commercial annual crops non-pivot	Transformed	16.4133	21.2157
Cultivated commercial annual crops pivot	Transformed	0	0
Cultivated commercial permanent orchards	Transformed	0.7326	1.1079
Cultivated subsistence crops	Transformed	30.2814	30.9555
Settlements	Transformed	31.9806	36.909
Mines	Transformed	1.0107	0.3393
Waterbodies	Transformed	0.918	2.5659
Bare Ground	Transformed	3.8358	19.9773
Degraded	Transformed	1.8018	1.6344
Total area intact (km^2)		**1767.3849**	**1607.1588**

Total area transformed (km²)	1444.9185	1391.5836
Total	3212.3034	2998.7424
Percentage intact	55.01923947	53.59442678

(d)

Habitat_MTP			
Land cover classes	**Intact/Transformed**	**Area_1990 (km²)**	**Area_2014 (km²)**
Low shrubland	Intact	54.8298	41.9643
Wetlands	Intact	176.7312	172.6974
Grasslands	Intact	3762.2817	3361.2984
Plantations / Woodlots	Transformed	3215.2662	3143.9682
Cultivated commercial annual crops non-pivot	Transformed	129.0015	128.4048
Cultivated commercial annual crops pivot	Transformed	1.2375	2.5074
Cultivated commercial permanent orchards	Transformed	5.0589	7.7319
Cultivated subsistence crops	Transformed	73.1961	74.0106
Settlements	Transformed	80.919	88.8849
Mines	Transformed	4.9077	7.6689
Waterbodies	Transformed	4.9545	7.317
Bare Ground	Transformed	9.0765	35.4159
Degraded	Transformed	5.8518	5.4702
Total area intact (km²)		**3993.8427**	**3575.9601**
Total area transformed (km²)		3529.4697	3501.3798
Total		7523.3124	7077.3399
Percentage intact		53.08622702	50.526895

(e)

Habitat_EquSS			
Land cover classes	**Intact/Transformed**	**Area_1990 (km²)**	**Area_2014 (km²)**
Low shrubland	Intact	25.1991	23.5719
Wetlands	Intact	41.9508	42.0003
Grasslands	Intact	1487.4777	1351.0395
Plantations / Woodlots	Transformed	1196.5824	1120.689
Cultivated commercial annual crops non-pivot	Transformed	14.5719	18.5445
Cultivated commercial permanent orchards	Transformed	0.8307	1.2051
Cultivated subsistence crops	Transformed	23.2668	23.7852
Settlements	Transformed	22.4532	25.605
Mines	Transformed	0.9243	0.3015
Waterbodies	Transformed	0.531	1.9503
Bare Ground	Transformed	3.2391	18.018
Degraded	Transformed	1.3275	1.2798

Total area intact (km^2)	**1554.6276**	**1416.6117**
Total area transformed (km^2)	1263.7269	1211.3784
Total	2818.3545	2627.9901
Percentage intact	55.16082523	53.90475786

(f)

Habitat_MaxSS			
Land cover classes	**Intact/Transformed**	**Area_1990 (km^2)**	**Area_2014 (km^2)**
Low shrubland	Intact	24.1461	22.5783
Wetlands	Intact	38.5677	38.412
Grasslands	Intact	1421.2269	1291.6161
Plantations / Woodlots	Transformed	1134.5193	1060.8948
Cultivated commercial annual crops non-pivot	Transformed	14.0724	18.0486
Cultivated commercial permanent orchards	Transformed	0.6534	0.8514
Cultivated subsistence crops	Transformed	20.5092	21.0348
Settlements	Transformed	21.2733	24.1299
Mines	Transformed	0.9171	0.2727
Waterbodies	Transformed	0.4824	1.881
Bare Ground	Transformed	3.1212	17.1693
Degraded	Transformed	1.2825	1.2645
Total area intact (km^2)		**1483.9407**	**1352.6064**
Total area transformed (km^2)		1196.8308	1145.547
Total		2680.7715	2498.1534
Percentage intact		55.35498643	54.14424911

(g)

Species_records_MTP			
Land cover classes	**Intact/Transformed**	**Area_1990 (km^2)**	**Area_2014 (km^2)**
Low shrubland	Intact	72.873	69.5952
Wetlands	Intact	244.2627	239.7411
Grasslands	Intact	4991.5323	4355.0649
Plantations / Woodlots	Transformed	3608.2242	3551.6934
Cultivated commercial annual crops non-pivot	Transformed	197.3979	199.2195
Cultivated commercial annual crops pivot	Transformed	2.3247	6.3909
Cultivated commercial permanent orchards	Transformed	5.1156	7.272
Cultivated subsistence crops	Transformed	114.0111	111.0816
Settlements	Transformed	140.571	153.3321
Mines	Transformed	7.0083	12.5541
Waterbodies	Transformed	11.9646	12.78
Bare Ground	Transformed	10.1961	48.7539

Degraded	Transformed	24.237	32.7699
Total area intact (km^2)		**5308.668**	**4664.4012**
Total area transformed (km^2)		4121.0505	4135.8474
Total		9429.7185	8800.2486
Percentage intact		56.29720548	53.00306175

(h)

Species_records_EquSS			
Land cover classes	**Intact/Transformed**	**Area_1990 (km^2)**	**Area_2014 (km^2)**
Low shrubland	Intact	37.2672	39.1797
Wetlands	Intact	77.3955	77.5548
Grasslands	Intact	2239.1343	2012.2227
Plantations / Woodlots	Transformed	1458.4419	1376.8812
Cultivated commercial annual crops non-pivot	Transformed	34.9839	39.8601
Cultivated commercial annual crops pivot	Transformed	0	0.5877
Cultivated commercial permanent orchards	Transformed	0.7596	1.1367
Cultivated subsistence crops	Transformed	53.8227	52.4565
Settlements	Transformed	58.635	66.2544
Mines	Transformed	1.9791	0.774
Waterbodies	Transformed	1.728	3.4596
Bare Ground	Transformed	4.689	25.5861
Degraded	Transformed	9.0801	17.8173
Total area intact (km^2)		**2353.797**	**2128.9572**
Total area transformed (km^2)		1624.1193	1584.8136
Total		3977.9163	3713.7708
Percentage intact		59.171607	57.32602561

(i)

Species_records_MaxSS			
Land cover classes	**Intact/Transformed**	**Area_1990 (km^2)**	**Area_2014 (km^2)**
Low shrubland	Intact	33.8877	35.1369
Wetlands	Intact	59.1507	59.5251
Grasslands	Intact	1956.8097	1756.1628
Plantations / Woodlots	Transformed	1208.016	1130.0724
Cultivated commercial annual crops non-pivot	Transformed	22.239	27.4059
Cultivated commercial annual crops pivot	Transformed	0.0072	0.5904
Cultivated commercial permanent orchards	Transformed	0.6093	0.9153
Cultivated subsistence crops	Transformed	40.7322	41.1417
Settlements	Transformed	42.714	49.3416

Mines	Transformed	1.6965	0.6012
Waterbodies	Transformed	1.4643	3.0447
Bare Ground	Transformed	3.7287	23.4711
Degraded	Transformed	7.6311	16.2189
Total area intact (km²)		**2049.8481**	**1850.8248**
Total area transformed (km²)		1328.8383	1292.8032
Total		3378.6864	3143.628
Percentage intact		60.66997221	58.87543946

Table S2.2 MaxEnt model performance across different background extents.

Scale	AUC Train	AUC Test	Threshold	Suitability threshold (≥)	Sensitivity	Specificity	TSS
Geopolitical boundaries	0.97	0.96	MTP	0.0686	0.94	0.81	0.76
			EquSS	0.1444	0.88	0.92	0.80
			MaxSS	0.1902	0.87	0.93	0.81
Species records	0.95	0.95	MTP	0.0699	0.96	0.75	0.71
			EquSS	0.1874	0.89	0.89	0.79
			MaxSS	0.2256	0.89	0.90	0.79
Habitat	0.94	0.93	MTP	0.058	0.94	0.64	0.59
			EquSS	0.1998	0.84	0.89	0.73
			MaxSS	0.213	0.84	0.89	0.74

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CHAPTER 3: Habitat occupancy of the cryptic berg adder, *Bitis atropos*, is related to topographic patterns of ambient energy

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Unpublished manuscript

"To be is to be perceived"

- **George Berkeley**

Abstract

Understanding habitat use is fundamental for the conservation and management of species. However, quantifying habitat use for small cryptic species is limited by incomplete detection during field surveys and the lack of habitat data at scales meaningful to the ecology of the species. Topographically-derived habitat variables from digital elevation models (DEMs) have the potential to overcome these limitations. This study used DEM-derived topographic variables as proxies for habitat conditions to study site-occupancy patterns of the berg adder (*Bitis atropos),* a small-bodied cryptic viper. Seven repeated field surveys were carried out in Buffelskloof Private Nature Reserve in the mountainous eastern parts of South Africa to estimate occupancy (Ψ) and detection

probability (*p*) using maximum likelihood methods. Although snakes occurred across a third of the available habitat (naïve occupancy = 0.283), they were only recorded as present a quarter (one in four visits to a sampling grid) of the time (*p* = 0.261). Occupancy was related to DEM-derived topographic covariates, which showed how snakes preferred north-west facing slopes, which are exposed to afternoon sun and presumably higher ambient energy. These results demonstrate the value of using DEM-derived topographic variables for ecological studies where habitat data are either unavailable or inappropriate, thereby providing valuable insights into habitat use of cryptic and difficult to detect species.

Keywords: cryptic; imperfect detection; occupancy modelling; site-occupancy.

Introduction

Understanding the factors affecting species' habitat use is not only central to ecology, but also fundamental to guiding conservation and management (Frey *et al.* 2012; Shelton *et al.* 2017). Habitat occupancy is generally regulated by various ecological factors, including climate, biotic interactions, and historical processes linked to dispersal (Chen *et al.* 2013; Cunningham *et al*. 2016). The extent to which these factors influence occurrence patterns is, however, dependent upon both the scale of assessment and the ecological requirements of specific species (Lyet *et al.* 2013; Cunningham *et al.* 2016; Michael *et al.* 2017). For example, although environmental factors explain species diversity at large spatial scales, the precise quantitative relationship differs amongst taxonomic groups (Hawkins *et al.* 2003). This is particularly true for ectotherms, like snakes, for which ambient energy (temperature) and moisture have been shown to be

important determinants of species occurrence patterns at large scales (Terribile *et al.* 2009; Lewin *et al.* 2016).

Many snake species, however, have small geographic distributions and are often restricted to topographically heterogeneous landscapes (Turner & Branch 2014; Yousefi *et al.* 2015; Behrooz *et al.* 2015). In such landscapes, local variations in topography (elevation, aspect, and slope) can change rapidly across short distances and create fine-scale variations in the structure and the thermal quality of habitat patches (Leempoel *et al.* 2015; Lembrechts *et al.* 2018; Barton *et al.* 2019). The thermal quality of local habitat is particularly important for snakes, which rely on behavioural thermoregulation to regulate and maintain optimal physiological functions associated with reproduction, development, and locomotion (Chen *et al.* 2010; Guillon *et al.* 2013; Michel *et al.* 2013). Therefore, variations in the thermal quality of a landscape may not only influence and drive habitat occupancy patterns of snakes, but may ultimately affect individual survival and fitness (Lourdais *et al.* 2004; Barton *et al.* 2019; Paterson & Blouin-Demers 2018). Linking occupancy patterns to environmental conditions could yield valuable insights into population processes that affect habitat selection (Blevins & With 2011; Frey *et al.* 2012).

At broad spatial scales, studies on species occurrence patterns regularly use global climate datasets (Buschke *et al.* 2015). The environmental predictor variables associated with these datasets comprise pixels of average climatic conditions, typically interpolated at a resolution of 30 arc-seconds (~1km²) (Hijmans *et al.* 2005; Garcia *et al.* 2019). While this resolution is appropriate when studying broad-scale occurrence patterns, it may be too coarse to capture and explain species-environment relationships

at smaller scales (Lembrechts *et al.* 2018). Habitat features that promote species occupancy at local scales require fine resolution data that more accurately reflect species-specific traits (dispersal ability, body size, and home range) (Garcia *et al.* 2019). This is especially true for mountainous areas, where micro-topographic changes in landscapes shape important habitat features that would be masked by coarse-scale environmental data (Leempoel *et al.* 2015; Barton *et al.* 2019). Consequently, climate data used to infer species distribution patterns at large scales might be inappropriate for studying species at smaller scales.

An alternative approach is to infer environmental conditions from topographically-derived terrain attributes from digital elevation models (DEMs) (Leempoel *et al.* 2015; Wang *et al.* 2016). These models are widely used in ecological studies where they capture the underlying biophysical processes linked to species occurrence patterns, even in topographically heterogeneous landscapes (Leempoel *et al.* 2015; 2018). DEMs provide further advantages, such as being at finer resolutions than those commonly used from interpolated climate datasets (Leempoel *et al.* 2015; Kropáček *et al.* 2018).

Terrain attributes derived from DEMs can be classified into two categories: primary terrain attributes (e.g., aspect, slope, elevation, and hillshade) and secondary terrain attributes (e.g., terrain ruggedness, wetness indices, and temperature indices) (Leempoel *et al.* 2015*)*. Secondary terrain attributes are calculated as derivatives or as combinations of primary terrain attributes (Leempoel *et al.* 2015). They represent variables of higher complexity and explanatory power and are therefore often used as proxies for environmental variables in combination with primary derived terrain attributes (Leempoel *et al.* 2015).

Given the potential of using DEM-derived topographic variables as environmental proxies, linking them to snake occupancy patterns remains challenging. This is largely because snakes are cryptic, exhibit stochastic activity patterns, and often inhabit difficult-to-survey terrain (Durso *et al.* 2011; Hansen *et al.* 2017). These considerations constrain detectability and create uncertainty when collecting occurrence records (Steen 2010). In light of this, it is unsurprising that snakes are regarded as one of the most difficult-to-study reptile groups (Durso *et al.* 2011; Sosa & Schalk 2016). Therefore, any study attempting to link snake occurrence patterns to habitat features must account for imperfect detection by estimating their detection probability (Mazerolle *et al.* 2007; Steen 2010). In this sense, occupancy models based on maximum likelihood methods have been widely used in studies interested in quantifying site-occupancy patterns of snakes while accounting for imperfect detection (Durso *et al.* 2011; Bonnet *et al.* 2016).

This study applies an occupancy modelling approach to evaluate habitat use by the berg adder, *Bitis atropos*. Berg adders are diurnal, small-bodied cryptic viperids, with a broad, but fragmented, geographic distribution in South Africa and also occur in isolated parts of the eastern highlands of Zimbabwe and Mozambique (Branch 1998). In South Africa, populations along the north-eastern escarpment are restricted to moist high-elevation montane grasslands (Haagner & Hurter 1988). As for most snake species in South Africa, quantitative demographic information at the population level remains largely unknown and insufficiently studied (Maritz & Alexander 2012a; Maritz & Alexander 2012b; Tolley *et al.* 2019). Although their dispersal potential is unknown, they are likely to have small home ranges and low vagility, similar to other species of dwarf adders (Maritz & Alexander 2012a; 2012b; Behrooz *et al.* 2015; Maritz *et al.* 2016).

Berg adders display traits that make them difficult to detect (e.g. narrow home ranges, small bodies, and sedentary lifestyles), so they may often be overlooked during ecological surveys. Therefore, this study first set out to carry out repeated surveys to simultaneously estimate site-occupancy (Ψ) and detection probability (p). This allowed us to quantify habitat usage while accounting for imperfect detection. Next, occupancy was linked to topographically derived habitat variables to infer the environmental variables that affect habitat usage by these snakes. This approach yielded not only conclusions about the applicability of using DEM-derived topographic variables as environmental surrogates, but also provided insights into the underlying ecology of this cryptic snake species.

Materials and methods

Study area

This study took place at Buffelskloof Private Nature Reserve (BKPNR; 25.283° S, 30.505° E; Figure 3.1), a small (*c.* 1500 ha), privately-owned and administered protected area, located on the eastern escarpment of Mpumalanga, South Africa. The reserve is embedded in a matrix of pine (*Pinus* spp.) and eucalypt (*Eucalyptus* spp.) plantations, which have replaced large portions of natural vegetation. As a result of historical habitat transformation, the remaining intact habitat of BKPNR primarily consists of a mosaic of moist montane grassland patches, interspersed with small shrub-like trees (*Protea* spp.) on the upper slopes and indigenous Afromontane forest belts along the ravines and valley bottoms. BKPNR is topographically complex, ranging from 1150 m to 1850 m in elevation and intersecting three natural vegetation biomes:

Grassland, Savanna, and Forest (Mucina & Rutherford 2006). It receives summer rainfall (October through February), characterized by frequent mist in the mornings and cold winters with occasional frost (Mucina & Rutherford 2006). Variations in elevation across the reserve directly affect moisture gradients, and the higher northern parts of the reserve are typically wetter than the drier southern parts.

Repeated field surveys

After accounting for the known habitat preferences of berg adders from the Mpumalanga escarpment (Haagner & Hurter 1988), surveys were restricted to short high-elevation montane grassland patches along the northern parts of the reserve. This area was overlaid with a regular grid (100x100 m) consisting of 219 individual sampling units (Figure 3.1) using the "grid index feature" function within ArcGIS 10.6 (ESRI 2015). The elevation of these units ranged between 1440 m and 1830 m. Grid size was selected based on the assumption that berg adders have small home ranges similar to those of a different, clade-related small-bodied congener, *Bitis schneideri* (Maritz & Alexander 2012a; Barlow *et al.* 2019).

To account for imperfect detection and potential bias of occupancy estimates, seven repeated field-surveys were conducted for each of the 219 sites between October 2016 and September 2017. Each repeated survey required between 15 and 20 days to complete and surveys were conducted at least one month apart.

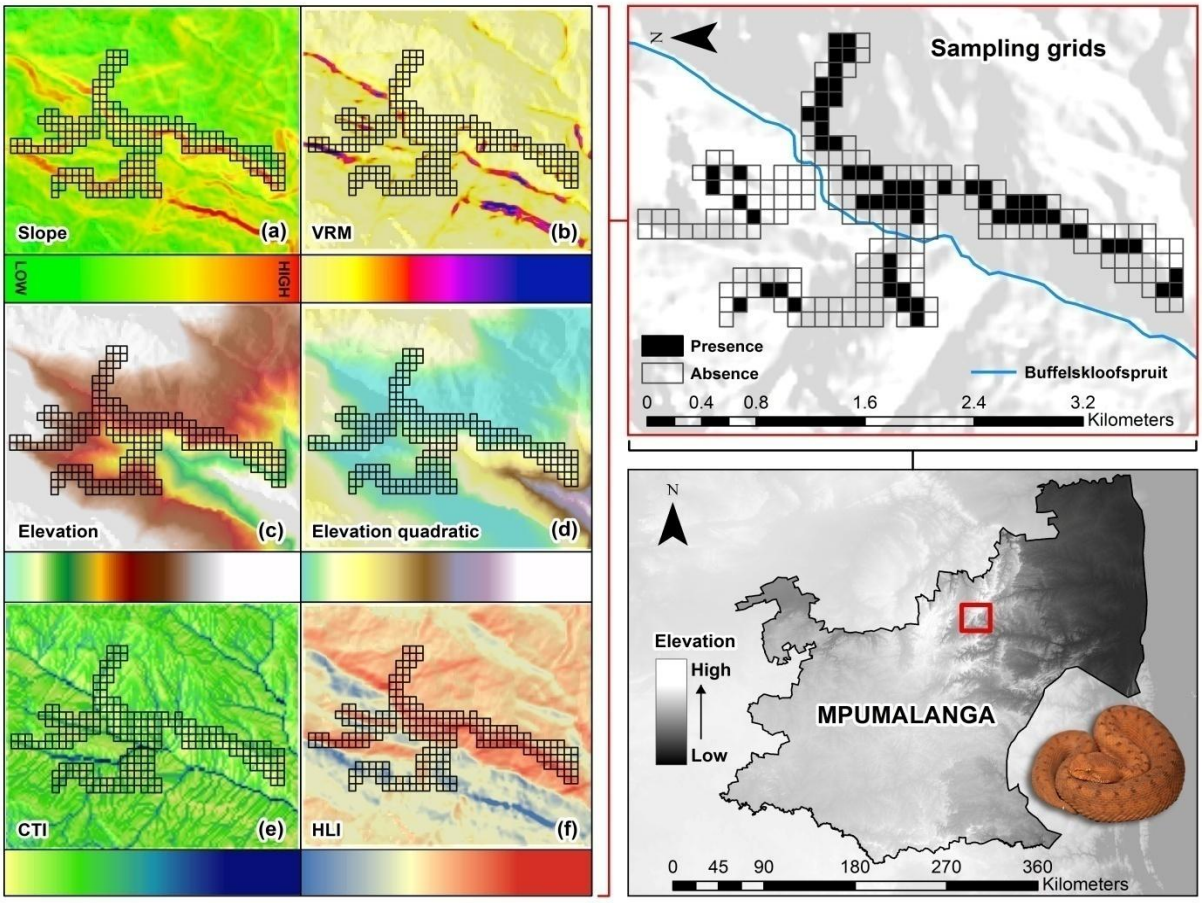

Figure 3.1 The location of the study area (top-right panel) in relation to South Africa's Mpumalanga province (bottom-right panel). The top-right map panel shows the cumulative detection/non-detection history for all sampling grids surveyed between 2016 and 2017. Map panels on the left (a-f) show the topography-derived variables that were related to berg adder occupancy patterns at BKPNR. Variables included were: (a) Slope, (b) Vector Ruggedness Measure, (c) Elevation, (d) Elevation quadratic, (e) Compound Topographic Index, and (f) Heat Load Index.

Surveys were performed between 07:00h and 18:00h under favourable conditions and on days without heavy rainfall or thunderstorms. Each sampling unit was surveyed according to an active search strategy for a minimum of 20 minutes. This entailed a random screening of the site and then lifting and searching underneath any loose, non-embedded, physical structures (logs and rocks) within the otherwise homogenous

grassland habitat and recording the presence of any encountered snakes. Refuges from overturned structures were also inspected for the presence of snakes.

Topography-derived habitat variables

This study derived six topography-derived habitat variables (Figure 3.1) from a Shuttle Radar Topography Mission (SRTM; Jarvis *et al.* 2008) digital elevation model (DEM) at a resolution of 1 arc second (~30m) using ArcGIS 10.6 (ESRI 2012). To ensure independence among the variables, the effect of collinearity between variable pairs was assessed in R version 3.4.3 (R Core Team 2017) using the "corrplot" package (Wei *et al.* 2017). Variables were deemed highly collinear when Pearson's $r \geq |0.7|$; however, all variables were below this threshold (Supporting information: Figure S3.1, p.90) and subsequently retained for modelling purposes. Zonal statistics were then used in QGIS (QGIS Development Team 2018) to calculate and extract mean values within each sampling unit.

Since the extracted mean grid values of predictor variable coefficients differed both in units of measure and numerical range, all variables were mean-centred and scaled by standard deviation using the "scale" function in R version 3.4.3 (R Core Team 2017). The topographic-derived environmental predictor variables consisted of primary (elevation, quadratic elevation and slope) and secondary (Vector Ruggedness Measure, Compound Topographic Index and Heat Load Index) terrain attributes selected with the *a priori* assumption of being important habitat drivers of berg adder occupancy (Table 3.1).

Table 3.1 Description of environmental predictors used to model site-occupancy patterns of berg adders at BKPNR.

Terrain attribute	Variable	Code	Description	Units	Ecological justification	Reference(s)
Primary	Elevation	ELEV	Height above sea level	m	Variability in elevation can facilitate the formation of distinct microclimates which may affect habitat occupancy patterns	Yousefi *et al.* (2015)
	Quadratic Elevation	ELSQ	Height above sea level squared	adimensional	Habitat preferences may be elevation-specific i.e. unimodal	Sadoti *et al.* (2013)
	Slope	SLO	Represents the rate of change in elevation as a function of rise over run to provide a measure of terrain steepness	degree (˚)	Slope inclination can facilitate or impede movement between habitat patches and also affect water availability and amount of solar exposure	Brito *et al.* (2011)
Secondary	Vector Ruggedness Measure	VRM	A multidimensional metric of terrain ruggedness which incorporates both slope and aspect as factors to determine local variation in topography	adimensional	Terrain ruggedness can influence habitat characteristics which may facilitate or impede behavioural thermoregulation and dispersal ability between habitat patches	Sappington *et al*. (2007); Wright *et al.* (2005)
	Compound Topographic Index	CTI	A steady-state measure of wetness based on underlying topography expressed as a function of slope and the per unit width of the upstream contributing area	adimensional	Moisture availability affects both vegetation characteristics and net primary productivity which may influence food availability	Gessler *et al.* (1995); Evans *et al.* (2014)
	Heat Load Index	HLI	A proxy for the potential ambient energy a site receives based on the underlying topography of the landscape	adimensional	Ambient temperature is important for optimal physiological functioning in ectothermic vertebrates and a known limiting factor of snake distributions	McCune and Keon (2002); Lewin *et al.* (2016)

Variables associated with primary terrain attributes included slope (SLO), elevation (ELEV), and quadratic elevation squared (elevation-squared: ELSQ). Slope affects the ability of species to move to up and down a hillside in response to changing climate conditions and inclination may also affect solar exposure. Elevation was regarded as an important variable in shaping microclimate availability, given that temperature-dependent environmental changes are known to be linked to elevation. The quadratic term for elevation was included to account for potential temperature-related mid-elevation (unimodal) effects on occupancy.

The secondary terrain variables represented variables of higher complexity and included Compound Topographic Index (CTI), Vector Ruggedness Measure (VRM), and Heat Load Index (HLI) (McCune & Keon 2002). CTI, which represents a measure of surface moisture, was calculated using the Geomorphometry and Gradient Metrics Toolbox (Evans *et al.* 2014). VRM, which represents fine scale topographic complexity and roughness, was calculated using Benthic Terrain Modeler (Wright *et al.* 2005) with a 3 x 3 neighbourhood to capture fine scale topographic variability. HLI is a multidimensional metric that integrates slope, aspect (folded around the north-east to south-west line), and latitude to represent a steady-state measure of slope thermal quality based on the potential amount of heat a site receives through incoming solar radiation (McCune & Keon 2002). The degree of incoming solar radiation a slope receives directly influences temperature and moisture, which affects local microclimatic conditions and therefore the behavioural thermoregulation of snakes. Because this study was conducted in the southern hemisphere, and the insolation characteristics of slopes differ between the northern and southern hemispheres, the heat load index

equation of McCune & Keon (2002) was adapted by using a modified formula to calculate the folded aspect (Folded aspect = | 180 - | Aspect - 315 ||) where aspect is folded around the south-east north-west line. In the southern hemisphere, northwest-facing slopes receive the greatest exposure to incoming solar radiation and therefore represent hotter and drier habitat conditions (McCune & Keon 2002; McCune 2007). In contrast, southeast-facing slopes represent habitats with cooler microclimates and higher levels of moisture; this is because they receive considerably less solar exposure, which reduces the desiccation rates. In this study, these differences were also reflected in the general vegetation structure, wherein grassland habitat is shorter and less dense on the northwest-facing slopes relative to the southeast-facing slopes.

Data analysis

To understand how landscape features might affect berg adder occurrence patterns, a standard maximum likelihood approach was adopted to fit single-season occupancy models (MacKenzie *et al.* 2002) using the “occu” function from the “unmarked” package (Fiske & Chandler 2011) implemented in R. This procedure estimated detection probability (p) and occupancy (Ψ) while considering the topography-derived explanatory covariates. Two important assumptions of single-season occupancy models are that populations (i.e., occupancy of sampling units) are closed during surveys and that false detection (i.e., species misidentifications) does not occur at a sampling unit when a species is truly absent (MacKenzie *et al.* 2002, Durso *et al.* 2011). We assumed that no false detections occurred based on two factors: (1) berg adders have distinct morphological features, and (2) the standardized method in which we conducted surveys always placed us in direct contact with snakes, which made positive

identification possible. In instances where the closure assumption may not be met (e.g. species with large home ranges and deterministic movement patterns) it may be relaxed when movement between sampling units are random during a survey period (Mazerolle *et al.* 2007; Jeffress *et al.* 2011). Because we assumed that berg adders have low vagility and small home ranges, we considered the assumption of closure to be met, and that non-detection at previously occupied sites were due to inherent species traits.

Given that the dataset was large (number of sites = 219) with few predictors, and because this study was primarily interested in quantifying the relationship between the proportion of sampling units occupied (naïve occupancy ignoring detection probability) and explanatory covariates, a general model (global model) was created for occupancy. The global model was based on an *a priori* assumption that the probability of detecting (*p*) a snake when present was constant throughout sampling sites and was unaffected by environmental variables because of the homogeneity of grassland habitat and the structured, standardized protocol used during field surveys. Therefore, only occupancy was permitted to vary with covariates, and detection probability (*p*) was held constant across space and time. Detection probability was reported as back-transformed values and represents the predicted mean ± standard error (*SE*) across all sampling occasions over the entire study period.

Results

Across the sampling period, berg adders were detected at 62 of the 219 sampling units, resulting in a naïve occupancy estimate of 0.283. However, in these 62 sites, the snakes were detected a variable number of times. Berg adders were recorded only

once in 31 of the sampling units and twice in 12 of the sampling units. Berg adders were only recorded three or more times in only 19 of the 62 occupied sites. This demonstrates that these snakes were not always detected even when they were present at a sampling unit. This general pattern was confirmed by estimates of detection probability, which was low (p = 0.261 ± 0.024 *SE*) and suggests that there is only a one in four chance of detecting a snake when present. Detection estimates showed that substantial effort is required to accurately assess occupancy, which justified repeated surveys for this cryptic and difficult to detect species.

Our global occupancy model, which considered site-occupancy to vary as a function of topographically derived covariates, showed that most of the variables were not significantly associated with occupancy. Elevation showed a generally positive relationship to occupancy, but this variable was marginally not significant (P = 0.0692). The only variable that was statistically significant and closely related to berg adder occupancy patterns was the heat load index (Figure 3.2; Supporting information: Table S3.1, p.90). The heat load index predicted that berg adder occurrence patterns were non-random and that occupancy was positively linked to the thermal characteristics of the landscape. Although the proportion of sites occupied by the snakes was approximately 28% (naïve occupancy), berg adders showed a clear preference for sites with higher thermal characteristics with occupancy generally increasing toward northwest-facing slopes that have higher heat load index values.

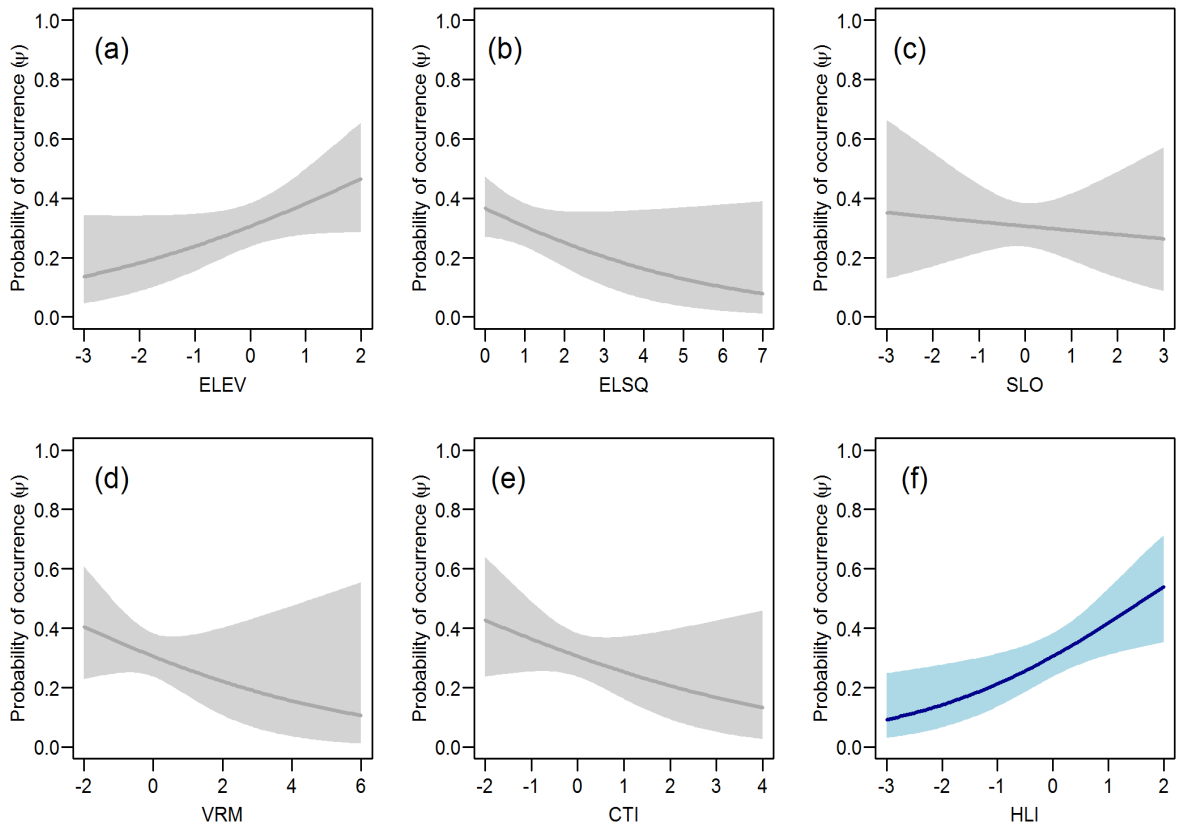

Figure 3.2 Predicted relationships between probability of occupancy (Ψ) and DEM derived environmental variables (a-f) for *Bitis atropos* at BKPNR on South Africa's Mpumalanga escarpment. Statistically significant (α = 0.05) relationships are shown in blue while non-significant relationships are shown in grey. Shaded areas represent the 95% confidence interval for both monotonic and unimodal response curves.

Discussion

Understanding species' habitat requirements is fundamental for their conservation and management (Frey *et al.* 2012; Shelton *et al.* 2017). Snakes are among the most difficult to study reptiles because they are difficult to detect and often occur in habitats that are difficult to survey (Durso *et al.* 2011; Sosa & Schalk 2016). Robust methods that consider imperfect detection are needed when studying snake habitat-use

(Mazerolle *et al.* 2007; Steen 2010). In this study, we assessed the habitat preferences of a small-bodied montane viperid (*Bitis atropos*) at the scale of a local nature reserve in the mountainous regions of the Mpumalanga escarpment, South Africa. We accounted for imperfect detection and found that berg adder occupancy patterns were non-random and associated with landscape characteristics linked to higher ambient energy.

Heat load index was positively associated with berg adder occupancy. This suggests that berg adders prefer habitats with certain thermal qualities. Specifically, occupancy was higher on north-west facing slopes, which receive prolonged daily exposure from incoming solar radiation and higher ambient energy (i.e. warm midday and afternoon sunshine). This is consistent with the findings of previous studies showing that patterns of habitat use by snakes are largely dependent on landscape characteristics that provide thermally conducive environments related to behavioural thermoregulation (Weatherhead & Charland 1985; Blouin-Demers & Weatherhead 2001). Furthermore, by occupying specific areas within a habitat that provide higher thermal quality may not only prove to be beneficial for optimal physiological-behavioural functioning of snakes but can also directly affect individual fitness (Blouin-Demers & Weatherhead 2008). For example, Halliday & Blouin-Demers (2016) showed that open field habitat patches with high thermal quality provide greater fitness benefits in terms of increased reproductive outputs and growth rates in colubrid snakes than habitats with characteristically lower thermal qualities. Therefore, the motivation for berg adders to use habitat patches based on their thermal characteristics may be encouraged by similar fitness-related proxies that depend on effective behavioural thermoregulation. Similar trends highlighting the importance of thermal quality on habitat use of snakes have also been

shown for black rat snakes (*Elaphe obsoleta obsoleta*) (Weatherhead & Charland 1985; Blouin-Demers & Weatherhead 2001), which actively select habitat edges with greater exposure to incoming solar radiation for thermoregulatory reasons.

The fact that berg adders show a clear preference for topographic areas supporting higher ambient energy is to be expected considering that thermoregulation is regarded as the most important proximate factor motivating squamate habitat use (Blouin-Demers & Weatherhead 2001; 2002). Viviparous snakes, such as *B. atropos,* depend on habitats that promote higher body temperatures during gestation and the fitness and phenotype of their offspring is directly affected by the temperatures experienced during development (Blouin-Demers & Weatherhead 2001). Therefore, if the conservation of berg adders is an objective, landscape areas supporting higher ambient energy should be targeted by management and planning efforts.

Additionally, our results showing berg adder habitat preferences are related to ambient energy is also consistent with previous studies showing the importance of ambient energy to reptile distributions at larger spatial scales (Terribile *et al.* 2009; Lewin *et al.* 2016). Not only does the positive association between occupancy and HLI show that berg adder distributions seem to be regulated by the same environmental variables at different spatial scales, but it also demonstrates the value of secondary derived terrain attribute variables when inferring species habitat-environment relationships at small scales when data are either unavailable or inappropriate.

Snakes have traits that limit their detection during field surveys, so assessments of habitat use are difficult to make without considering imperfect detection (Mazerolle *et al.*

2007; Steen 2010). Our results confirm this by showing that berg adder detection probability was low (p = 0.261). Despite often being found at high population densities (Phelps 2010), these snakes are easily missed during surveys due to their cryptic colouration and small body size. Similarly, our estimated detection probability is in accordance with the findings of other studies that emphasize the difficulty to study snakes, especially vipers, in natural settings (Maritz *et al.* 2016; Bauder *et al.* 2017). Low detection probability highlights the need to conduct multiple repeated surveys to establish the presence of berg adders. This also applies to other southern African reptiles because detailed population studies that consider imperfect detection remains a critical research gap to inform regional conservation assessments (Tolley *et al.* 2019).

Topographically heterogeneous landscapes are known to affect the thermal characteristics of habitats (Leempoel *et al*. 2015; Lembrechts *et al.* 2018; Barton *et al.* 2019). Mountain environments provide considerable challenges for ectotherms that rely on ambient energy to maintain optimal physiological functions. Habitat suitability is related to areas of greater thermal suitability based on specific landscape characteristics. Given that mountain habitats provide a wide variety of microhabitats, ectothermic species would favour habitats that facilitate behavioural thermoregulation. Our study supports this view, because the small-bodied berg adder favoured north-west facing slopes that had a higher heat load index. Therefore, physical topographic variables can be used as reliable proxies for abiotic variables, which can then be linked to species occupancy patterns.

Although our study did not find statistically significant associations between other topographic variables despite an expected relationship, we should not disregard these

variables as being important to snakes. It may be that the association between habitat use and terrain are scale-dependent. For example, moisture (CTI) may still be relevant, but at spatial scales more closely related to snake osmoregulation. Similarly, despite VRM not being positively associated to berg adder habitat preferences in our study, habitat heterogeneity is generally considered an important factor for micro-habitat selection in snakes (Blouin-Demers & Weatherhead 2001; 2008; Harvey & Weatherhead 2010; Steen *et al.* 2014). Factors influencing habitat use might not be consistent across scales (McGill 2010), so it is important to match the scale of predictor data to the ecology of the species when studying habitat preferences (Guisan & Thuiller 2005).

Our study provides insights into the habitat requirements of berg adders, a species challenging to detect and monitor. We were able to couple occupancy preferences to landscape features using DEM derived topographic variables as environmental proxies in a way that provide meaningful biological insights. In this regard, DEM-derived topographic variables can be valuable proxies when environmental data are unavailable or at inappropriate scales. However, our repeated surveys have shed light on the imperfect detection of cryptic species, where specimens are more likely to be missed than recorded in their preferred habitats. Therefore, although DEM derived topography variables can stand in for sparse environmental data, thorough field surveys remain essential when studying species habitat use.

Acknowledgements

We thank the National Research Foundation (NRF) for providing financial support to Prof. N. Heideman (grant no. IFR150216114248) and for awarding A. Jordaan with an Innovation Scarce Skills Development Masters Scholarship. Permits to carry out this research were obtained from the Mpumalanga Tourism and Parks Agency (MTPA) under permit no. MPB. 5571/2, and ethical clearance was provided by the University of the Free State's Animal Ethics Committee (clearance no. UFS-AED2016/0115).

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Supporting Information: Chapter 3

Table S3.1 Global occupancy model β-parameter estimates for DEM derived environmental variables.

Parameter	Estimate	*SE*	*z*-value	*P*(>|*z*|)
Intercept	-0.5496	0.227	-2.423	0.0154
ELEV	0.3409	0.188	1.817	0.0692
ELSQ	-0.2729	0.165	-1.656	0.0977
SLO	-0.0691	0.214	-0.323	0.7467
VRM	-0.2182	0.196	-1.113	0.2658
CTI	-0.2625	0.211	-1.245	0.2130
HLI	0.4885	0.184	2.652	0.0080*

*Statistically significant ($P < 0.05$) effect on site-occupancy.

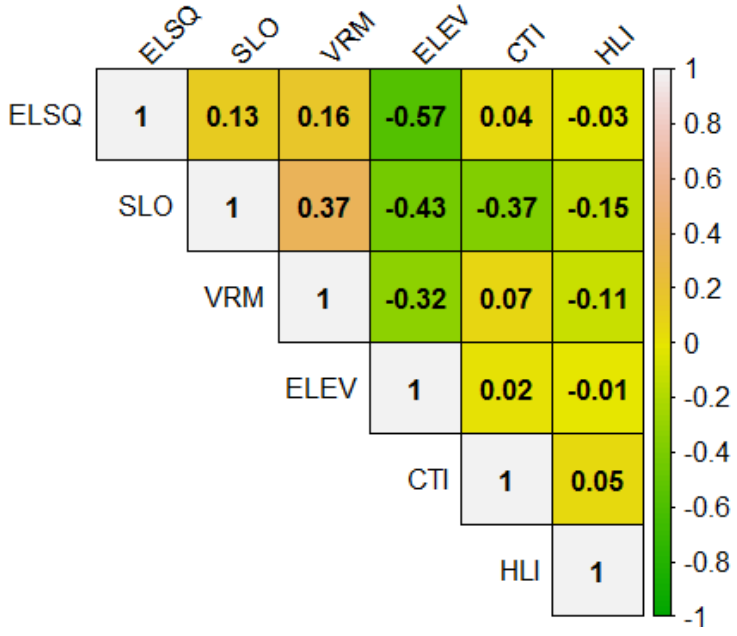

Figure S3.1 Matrix of pairwise correlation coefficients for DEM-derived environmental variables used in predicting occupancy relationships for berg adders.

CHAPTER 4: General Conclusion

Despite being the most diverse group of terrestrial vertebrates, reptiles are relatively understudied compared to amphibians, birds and mammals (Roll *et al.* 2017). This is exacerbated by the rapid rate of new species descriptions as new reptiles are discovered, and existing species complexes are revised (Meiri & Chapple 2016; Tolley *et al.* 2016). In this thesis, I explored patterns of geographic distribution and habitat use of the Mpumalanga berg adder, *Bitis atropos*, which represents an evolutionary distinct lineage of a larger species complex (Kelly *et al.* 2011). In Chapter 2, I showed that this lineage would likely be classified as (at least) "Vulnerable" based on IUCN criteria due to its restricted range size and continued habitat loss within its distribution. In Chapter 3, I studied habitat use at the scale of a nature reserve and showed that even through snake detection was low during field surveys, snakes clearly favoured habitats where topography supported higher ambient energy. By combining these lines of evidence, this thesis contributes a deeper understanding to the spatial ecology of this snake by providing baseline information about its distribution and habitat requirements, which can help support conservation decisions that may arise post-completion of the pending taxonomic revision.

The modelled geographic range size estimates in chapter 2 indicated that if berg adders undergo a taxonomic split that it is likely that the lineage representing the current Mpumalanga population would immediately be threatened and would require a change in their conservation status from the current "Least Concern" status to "Vulnerable".

These results were consistent across all models, despite differences in the way in which geographic background extents were selected. The most important source of variation in predicted range size estimates between models resulted from the method used to delineate range margins. This finding was consistent with previous findings that the choice of delineation threshold is a source of uncertainty in range size estimates (Nenzén & Araújo 2011). However, my approach considered this uncertainty of range size estimates by comparing several modelling thresholds and also geographic background extents. This allowed me to draw conclusions from aggregated estimates of geographic range size and also provided important insights into the sources of uncertainty that need to be considered when modelling range size estimates for conservation assessments.

Furthermore, my modelling approach provided insights into threatening processes because it showed that suitable habitat within the Mpumalanga berg adder's distribution range has declined by at least 9% over the last 24 years. The fact the habitat loss is ongoing provides somewhat worrying prospects if the Mpumalanga lineage is to be described as a new species, since habitat loss is considered the primary threat to African reptile species in general and narrow ranged habitat specialists in particular (Böhm *et al.* 2013; Tolley *et al.* 2016). Although my results suggest that the Mpumalanga berg adder is adequately represented by the current protected area network, it does not guarantee its persistence because protected areas usually have management plans that are centred on the protection of more charismatic taxonomic groups and reptiles generally receive scant attention in this regard (Roll *et al.* 2017). Importantly, even if the premise that the Mpumalanga berg adder might be classified as

a distinct taxonomic group turns out to not hold true, my general framework to assess taxonomically problematic taxa even before formal taxonomic resolutions, remains broadly relevant due to its generality and it being conceptually easy to implement. This approach could, therefore, provide a useful approach across taxonomic groups that suffer from incomplete knowledge.

Habitat use by berg adders at the scale of a local nature reserve showed that these snakes actively select areas with landscape characteristics that are more conducive to higher ambient energy by incoming solar radiation. In this respect, occurrence patterns were non-random with berg adders showing a clear preference for north-western facing slopes characterized by higher ambient energy. The selection of landscape areas based on thermal quality is unsurprising, considering that snakes rely heavily on favourable thermal conditions for behavioural thermoregulation to maintain optimal physiological functioning (Ayers & Shine 1997). Therefore, occurring in areas characterized by higher ambient energy might increase individual survival and ultimately fitness (Halliday & Blouin-Demers 2016; Paterson & Blouin-Demers 2018).

These findings are not only consistent with studies that show how temperature drives snake habitat-use patterns at local landscape scales (Weatherhead & Charland 1985; Blouin-Demers & Weatherhead 2001; Halliday & Blouin-Demers 2016), but is also congruent with previous findings at larger spatial scales (Lewin *et al.* 2016). These large-scale studies show that reptile distributions, and specifically snake distributions, across the whole of Africa are mainly constrained by temperature-related factors, such as ambient energy (Lewin *et al.* 2016).

Results presented in chapter 3 also demonstrated that secondary terrain attribute variables derived from finer scale digital elevation models (DEMs) might serve as appropriate surrogates for environmental variables that are generally only available at coarse global scales when studying snake occupancy patterns. The fact that the majority of DEM-derived covariates used in my analysis were not associated with habitat selection does not imply that these variables are unimportant for the biology of berg adders. This might instead reflect issues related to the scale at which these variables interact with the species ecology.

In addition to providing information related to habitat use, my findings also support previous studies that showed how snakes are difficult to detect due to their unique intrinsic and extrinsic traits (Durso *et al.* 2011). The results in chapter 3 showed that berg adders have a low detection probability and, therefore, require considerable effort to detect during field-surveys. This reiterates the importance of repeated surveys to discern a snake's presence or absences during habitat use studies (Durso *et al.* 2011; Bauder *et al.* 2017). This finding also implies that reserve managers should be aware that snakes might occur on their reserves even when they are not recorded regularly.

In this thesis, I provide a multi-scale assessment of the conservation status and habitat preferences for berg adders from the Mpumalanga escarpment. This work provides baseline information to inform management and conservation efforts across geographic scales and provides an important piece to a larger puzzle of dwarf adder ecology and reptile conservation in general.

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