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Ecology of the Namaqua Dwarf Adder, Bitis schneideri

Maritz, Bryan

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Ecology of the Namaqua Dwarf Adder, *Bitis schneideri*

Bryan Maritz

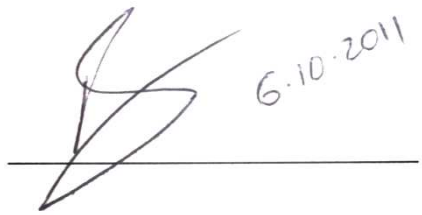
A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy

Johannesburg, South Africa

October, 2011

DECLARATION

I declare that this thesis is my own, unaided work unless specifically acknowledged in the text. It has not been submitted before for any degree or examination in any other university, nor has it been prepared under the aegis or with the assistance of any other body or organisation or person outside the University of the Witwatersrand, Johannesburg.



Bryan Maritz, 6 October 2011



"*The best of science doesn't consist of mathematical models and experiments, as textbooks make it seem. Those come later. It springs fresh from a more primitive mode of thought, wherein the hunter's mind weaves ideas from old facts and fresh metaphors and the scrambled crazy images of things recently seen. To move forward is to concoct new patterns of thought, which in turn dictate the design of the models and experiments. Easy to say, difficult to achieve*."

- E O Wilson (1992) *The diversity of life*

ABSTRACT

The loss of global biodiversity is exacerbated by the problem of trying to conserve species whose biology is not understood. The conservation of African snakes provides a striking example of this problem as many species remain entirely enigmatic. If we are to effectively manage or conserve these species, then we need to begin to describe and quantify their ecology. This project aimed to increase the body of knowledge regarding the ecology of *Bitis schneideri*, an arid-adapted African viperid, and as such, provide the basis for an informed critical assessment of the conservation status of the species. The improved understanding of the ecology of *B. schneideri* will contribute to the emerging study of African snake ecology, allowing scientists to compare and contrast the ecology of African snakes with those from northern temperate systems on which most of the global understanding of snake ecology is based.

Bitis schneideri is a species of very small-bodied viperids that grow rapidly and reach sexual maturity within the first two years. They are sexually dimorphic for several traits, and evidence suggests that fecundity selection has played an important role in shaping their morphology. Moreover, I suggest that the selective advantage of being able to bury into sandy substrates has resulted in the extreme body size displayed in the species. *Bitis schneideri* is diurnally active, a state that is probably a derived condition, as *B. caudalis* (the sister species to *B. schneideri*) is reported to be nocturnal. Additionally, *B. schneideri* shows seasonal variation in activity, with increased activity during the spring mating season. Activity during winter is reduced, but not absent, and appears to be governed by the availability of suitable environmental conditions. Activity in *B. schneideri* is limited at all temporal scales by environmental conditions. Radio-telemetry and mark-recapture analysis showed that *B. schneideri* is highly sedentary, moving between 0.8 ± 6.5 m.d^{-1} and 47.3 ± 3.9 m.d^{-1}, inhabiting small homeranges (♂: 0.85 ± 0.09 ha; ♀: 0.10 ± 0.09 ha). Moreover, juveniles show limited dispersal that, when combined with sedentary adult behaviour, could result in vulnerability to fragmentation by limiting gene-flow. Population densities are high (≈ 8 ha^{-1}) and survival is low (39% and 56% per annum) compared to viperids from other parts of the world. Additionally, juveniles have higher survival rates than adults. Small litter sizes imposed by small-bodies, and low survival, means that *B. schneideri* must reproduce frequently, probably annually, in order for populations to persist. Such frequent reproduction is atypical, even among closely related species, and in *B. schneideri*, appears to be facilitated through the capacity to feed year-round in the aseasonal habitat in which they occur. *Bitis*

schneideri is a generalist that ambushes prey in proportion to encounter frequency. Also, I show that the capacity of *B. schneideri* to capture and consume relatively large prey items provides snakes with a large energetic advantage. Abundant generalist predatory birds are likely to be more important predators of *B. schneideri* than are rare specialist predatory raptors, although snakes are also vulnerable to other predators that include small mammals, other reptiles, and large invertebrates.

Small body-size has two important implications for *B. schneideri* biology – reduced litter size, and vulnerability to a wide suite of predators. These attributes interact to result in low survival, reduced movement and dispersal, frequent reproduction, generalist foraging, and year-round feeding. *Bitis schneideri* is not at significant risk of facing extinction in the near future. The primary biological factor that ameliorates against extinction risk is large population size and high population density.

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CHAPTER 1

IN THE BEGINNING

1.1 Conceptual framework and problem identification

The loss of biodiversity globally has been recognized as one of the greatest challenges facing modern society (Wilson, 1992; Pimm et al., 1995; Myers et al., 2000). Anthropogenic utilization of resources has pressurized numerous systems to the point of collapse, and numerous ecosystems and ecosystem processes have been irreversibly altered, with resultant loss in integrity, function, and ecosystem goods and services (Folke et al., 1996; Jackson et al., 2001). Moreover, species extinctions, primarily as a result of anthropogenic impacts, are purportedly currently higher than ever in recorded history (Butchart et al., 2010).

Efforts to conserve biodiversity gained global recognition and became more formalized during 2002 with the formation of the Convention on Biological Diversity (CBD), wherein signatory countries pledged to significantly reduce the current rate of biodiversity loss by the year 2010 (Secretariat of the Convention on Biological Diversity, 2003). However, a recent meta-analysis has demonstrated that there is little evidence to suggest that a reduction in the loss of biodiversity has taken place at all, and that in fact, we are not close to meeting the objectives set out by the convention (Butchart et al., 2010).

One approach to combating the loss of biodiversity has been to target biodiversity hotspots as priorities for conservation and focus to conservation efforts in regions where those efforts can gain the greatest return on investment (Myers et al., 2000). Myers et al. (2000) recognized 25 biodiversity hotspots, among which southern Africa's Succulent Karoo was recognized as one of only two arid regions with exceptional levels of biodiversity.

Within the global biodiversity hotspots, conservation biologists have endeavoured to conserve biodiversity through concerted efforts to manage conservation needy species, and develop improved understanding of ecosystem function (e.g., Reyers et al., 2009), the function of particular species within ecosystems (e.g., Delibes-Mateos et al., 2007), and the likely responses of species to changes in those ecosystems (e.g., Midgley et al., 2002). As a result, many studies have attempted to describe, quantify, and understand the biology of species of conservation concern – as evidenced by the profusion and popularity of

conservation-orientated journals (e.g., Biological Conservation, Conservation Biology, Conservation Letters, Environmental Conservation, and Oryx).

While the number of studies describing the biology of species continues to grow, the available information is strongly outweighed by the number of species of conservation concern for which we require such information. This paucity of information thus provides one of the largest hindrances to modern conservation efforts – how do we conserve that which we do not understand?

The problem of trying to conserve what we do not understand is exacerbated by the fact that most of the earth's biodiversity occur in areas that are politically unstable (Hanson et al., 2009), and as a result are poorly investigated. It is thus unsurprising that Africa, with its long-standing political turmoil and significant biodiversity, remains a major challenge for conservation biology. Moreover, increasing human populations and the resultant pressure on ecosystems has resulted in African biodiversity facing significant pressure.

Finally, even though conservation biologists have made significant inroads to understanding the biology of many species, those investigations have not been evenly spread among taxonomic groups. As a result, certain groups (primarily mammals and birds) have received attention and funding disproportionately to their diversity, while other taxonomic groups, primarily "lower vertebrates" such as amphibians, reptiles, and fish, have received little attention (Bonnet et al., 2002a; Trimble & Van Aarde, 2010).

The snakes is one example of a taxonomic group that has been poorly investigated. This is partly because many people consider snakes to be poor model organisms for research (Turner, 1977; Huey et al., 1983). Seigel (1993) critically challenged this dogma, suggesting that such perceptions resulted from, among other factors, the inappropriate matching of research question, technique, and study species. In the years following Seigel's (1993) paper, at least one aspect of snake-oriented research, snake ecology and behaviour, has proliferated (Shine & Bonnet, 2000). Shine and Bonnet (2000) highlight some of the likely causes for the increase in snake ecological research, including but not limited to, advances in technology, changes in social attitudes, and increased funding availability.

One result of the increase in the number of studies focusing on snake ecology and behaviour is the emergence of several model organisms and model study systems. Work on *Crotalus horridus*, *C. viridis*, *Thamnophis sirtalis*, *Liasis fuscus*, *Hoplocephalus bungaroides*, and

Vipera berus have undoubtedly shaped our understanding of snake ecology. Notably, these species are restricted to North America, Europe, and Australia, and studies of African, South American, and Asian species are conspicuous by their absence.

A major challenge facing African biologists and conservation planners is the obvious gap in our understanding of the ecology of African snake species. The theory driving management of African snakes is by default based on species and systems that may be entirely inappropriate. Janzen (1976) hypothesised that African snake populations occur at lower population densities than snakes from equivalent habitats in other parts of the globe and suggested that such differences were the result of unique population drivers in Africa. Whether correct or not, Janzen (1976) highlights the potential that theory developed on the basis of non-African species, may be entirely inappropriate for understanding and managing populations of African snake species. In short, Africa is in desperate need of studies that describe and quantify the biology of African species.

1.2 Problem statement

The loss of global biodiversity is exacerbated by the problem of trying to conserve species whose biology is unknown. The conservation of African snakes provides a striking example of this problem as many species remain entirely enigmatic. If we are to effectively manage or conserve these species, then we need to study their ecology. Species that are already recognized as being of conservation concern provide an ideal initial focus. *Bitis schneideri*, a small arid-adapted viperid that occurs along the southern African west coast, has long been regarded as a species of conservation concern, yet our collective knowledge of its biology is meagre.

1.3 Aim

This project aims to increase the body of knowledge regarding the ecology of *Bitis schneideri*, an arid-adapted African viperid. In doing so, it will provide the basis for an informed critical assessment of the conservation status of the species. Additionally, the improved understanding of the ecology of the species will contribute to the emerging body of knowledge on African snake ecology and thus allows scientists to compare the ecology of African snakes with those from northern temperate systems on which most of the global understanding of snake ecology is based.

1.4 Choice of species

Several facets of the biology of *Bitis schneideri* make the species ideally suited to ecological research. Factors that influenced my decision to work on this species included: -

a) Abundance – *Bitis schneideri* was purported to be easily detectable and locally abundant. Seigel (1993) implicated sample size-related constraints as one of the major constraints to snake research, and one of the drivers of "lizard-envy".
b) Habitat – Many habitats are structurally complex, making field observation difficult. *Bitis schneideri* inhabits a structurally simple arid habitat that is easily accessible and logistically simple in which to work.
c) Size – *Bitis schneideri* is the smallest viperid (Branch, 1998). While the small body-size of individuals caused logistical constraints for the implantation of equipment, the species provided an ideal animal to investigate the evolution and ecological implications of small body size in snakes.
d) Conservation status – At the inception of this study, *Bitis schneideri* was listed as Vulnerable by the IUCN (World Conservation Monitoring Centre, 1996). This conservation status provided a strong motivation to study the species as findings could have important conservation implications.

1.5 Structure of this thesis

Chapter two presents data on the morphology, degree of sexual size dimorphism, and growth patterns in *B. schneideri*. Given that *B. schneideri* is the smallest viperid, such information can provide valuable insights into the evolution of extreme traits, and is also essential in understanding other aspects of the species' biology such as population dynamics, energetics, and reproductive biology. This chapter has been accepted for publication by Journal of Herpetology.

Chapter three investigates variation in activity patterns of my study population of *B. schneideri*. I present data collected using radio-telemetric techniques and field observations, and investigate the relative importance of environmental cues and internal motivations on patterns of activity. This chapter has been submitted for publication to Journal of Arid Environments.

Chapter four investigates the spatial ecology of *B. schneideri* through the use of mark-recapture techniques and radio-telemetry. More specifically, the chapter presents data on the variation in daily displacement during different seasons. This chapter has been accepted for publication by Copeia.

Chapter five uses mark-recapture analysis to estimate population density, survival, and recapture probabilities for *B. schneideri* populations at two sites. The chapter also quantifies and discusses the contribution of emigration to estimates of survival. This chapter has been submitted for publication to Herpetologica.

Chapter six investigates the reproductive biology of *B. schneideri* by estimating reproductive frequency in the context of body size constraints and low survival rates.

Chapter seven and eight provide insight into the relative trophic position of *B. schneideri*. Chapter seven uses data on the abundance of prey species collected using pitfall traps to estimate prey availability. I also discuss the impact of prey size and feeding frequency on the evolution of the ability to consume relatively large meals exhibited by many ambush predators. Chapter eight uses data published in the literature to assess the tendency for each of the various bird species on my study site to feed on *B. schneideri*, and quantifies the abundance of these species at the site. I use these measures to estimate the relative importance of each avian species as potential predators of *B. schneideri*. Chapter 8 has been published in African Zoology (Maritz & Scott, 2010).

Finally, chapter nine critically assesses a recent change in the conservation status of the species from Vulnerable to Least Concern, by providing a synthesis of how the separate chapters integrate to elucidate the ecology of *B. schneideri*. Additionally, this chapter assesses the recognised threats facing the species in the context of its ecology.

1.6 The status quo

1.6.1 The Namaqua Dwarf Adder, Bitis schneideri *(Boettger 1886)*

Taxonomy - Boettger (1886) described *Vipera Schneideri* from *Angra Pequenia* (= Luderitz Bay, Namibia). Later the species was synonymised with *Bitis caudalis*, before Haacke (1975) finally recognised *Bitis schneideri* as a full species on the basis of morphological characters. Recent preliminary molecular data indicate that *B. schneideri* is a valid species, but that *B.*

caudalis is polyphyletic relative to *B. schneideri* (W. R. Branch, *Pers. Comm.*). Research is underway to ascertain the taxonomic status of *B. caudalis* and *B. peringueyi*, and their phylogenetic relationships relative to *B. schneideri* (A. Barlow, *Pers. Comm.*).

Distribution - *Bitis schneideri* ranges from Luderitz, Namibia, southwards to coastal Namaqualand (Broadley, 1983; Branch, 1998). Boycott (1987) collected *B. schneideri* from the Oliphants River Settlement (3118CA). Recently, the South African Reptile Conservation Assessment (SARCA), using data from Broadley (1983), Boycott (1987), the CapeNature database, as well as the SARCA Virtual Museum (URL: http://vmus.adu.org.za/), showed that the species occurs almost continuously along the coastline, from Luderitz to the Olifants River Settlement (Fig. 1.1). The distribution of the species in Namibia is less well known. Broadley (1983) describes the species as occurring south of the Luderitz – Aus road (26° 30' S). It is also known from various scattered localities southwards to Oranjemund (Broadley, 1983) and I have observed *B. schneideri* near the Boegoeberg Mountains (2715DD). Limited access to the central parts of the Sperrgebiet has resulted in a dearth of locality data from this area, although it does contain suitable habitat (*Pers. Obs.*).

Feeding - Several species of small vertebrates have been recorded in the diet of *B. schneideri*. Broadley (1983) lists the geckos *Pachydactylus rangei* (as *Palmatogecko rangei*) and *Pachydactylus austeni*, as well as an unknown frog of the genus *Breviceps* (probably *B. macrops*) as prey items. Like other *Bitis* spp., *B. schneideri* is likely to be an ambush-forager as foraging mode appears to be phylogenetically conserved among snakes (Greene, 1997) and the snake's stout body form is typical of ambush foragers.

Reproduction – Namaqua Dwarf Adders are viviparous, producing between three and seven live young (Branch, 1998; Alexander & Marais, 2007).

Activity - Branch (1998) reports that Namaqua Dwarf Adders are likely to be nocturnal.

Conservation - MacLachlan (1978) listed *Bitis schneideri* as Rare (Restricted). Branch (1988) listed the species as Vulnerable in South Africa. The World Conservation Monitoring Centre (1996) listed the species as Vulnerable on the basis of suspected population declines resulting from habitat loss and exploitation. More recently however, the species has been re-evaluated as Least Concern by the Southern African Reptile Conservation Assessment (Bates et al., In Press), based on improved knowledge of the distribution of the species and information presented in this thesis.

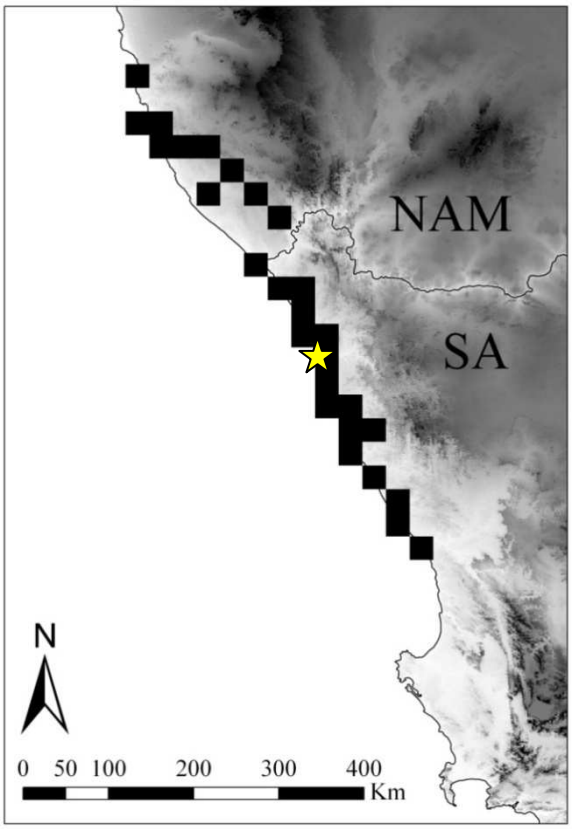


Figure 1.1: The distribution of *Bitis schneideri* at quarter degree square resolution. Data from Broadley (1983), Boycott (1987) and the CapeNature and SARCA databases (see text for details). The star represents the approximate location of my study site.

1.7 Study site

All data were collected along coastal dune fields on the farm Noup, Northern Cape Province, South Africa (30°08'S, 17°12'E). Noup forms part of Namaqualand Mines and the De Beers Diamond Route, but all dune habitats on the farm are relatively pristine. My study site was approximately rectangular in shape and approximately 480 ha in extent. The region receives 50 – 150 mm rainfall per annum, and coastal fog is frequent (Cowling et al., 1999). More than 60% of annual rainfall falls during winter (Desmet, 2007). Temperatures are cool year-round, ranging from a mean temperature of 14.3°C in winter to 18.2°C in summer (Desmet, 2007). The substrate primarily comprises recent calcareous aeolian sands that form semi-vegetated longitudinal dunes (Desmet, 1996; Desmet & Cowling, 1999). Vegetation is succulent or sclerophyllous as is typical for Sandveld habitats along the coast (Mucina &

Rutherford, 2006). Habitats on the farm comprise two major elements, semi-vegetated aeolian dune fields, and *Woolia faranosa*-dominated flatlands (Fig. 1.2). Although the species is occasionally found in the *Woolia faranosa*-dominated flatlands, it is more abundant in the dune cordons. My search efforts were thus concentrated in dune habitat which appears to constitute a source area for populations.



Figure 1.2: *Woolia faranosa*-dominated flatlands (left), and semi-vegetated aeolian dune fields (right) that made up the majority of available habitat on the farm Noup, Northern Cape Province, South Africa.

CHAPTER 2

MORPHOLOGY, SEXUAL DIMORPHISM, AND GROWTH IN THE SMALLEST VIPERID, *BITIS SCHNEIDERI* (REPTILIA: SQUAMATA: VIPERIDAE)

This chapter has been published as Maritz, B., and Alexander, G. J. In Press. Morphology, sexual dimorphism, and growth in the smallest viperid, *Bitis schneideri* (Reptilia: Squamata: Viperidae). Journal of Herpetology.

Abstract – Species that exhibit extreme traits can provide valuable insight into the evolution of those traits. *Bitis schneideri* has the smallest body size of all vipers, reportedly reaching a maximum length of 254 mm. We studied size, sexual size dimorphism, and growth in a population of *B. schneideri* from the Northern Cape Province, South Africa to better understand these traits in the smallest viperid. We weighed and measured 285 snakes (124 males, 101 females, 60 juveniles) over three austral summers. We recorded a maximum body length of 251 mm, and body mass of 38 g. Mean adult female body length (207.4 ± 27.6 mm) was longer than mean adult male body length (191.6 ± 20.2 mm). As predicted, female snakes were heavier bodied than males of the same length, had shorter tails, and had relatively larger heads. Growth rate was rapid and did not appear to differ among the sexes. Individuals reach mean adult body length in approximately 2.2 years, and male snakes are likely to reach reproductively mature size in approximately 10 months. We suggest that sexually dimorphic traits have evolved primarily through fecundity selection for females. Additionally, we propose that the evolution of small body size in *B. schneideri* is a result of the selective thermoregulatory, foraging, and predator avoidance advantages gained by being small enough to shuffle into sandy substrates.

2.1 Introduction

Organisms that exhibit extreme traits can be used to elucidate the selective pressures and evolutionary processes that have driven biological diversification (Secor & Diamond, 1998; Hedges, 2008). The study of such organisms is therefore valuable to science, especially in

cases where those organisms are from geographic regions or phylogenetic lineages that are understudied (Parker & Plummer, 1987; Shine & Charnov, 1992; Webb et al., 2002a; Hibbitts et al., 2005).

Bitis schneideri (Namaqua Dwarf Adder) is a species of small viperid snakes that inhabit arid habitats along the west coast of southern Africa (Broadley, 1983; Branch, 1998). Adult snout-vent length (SVL) is reported to reach 254 mm (Branch, 1998), making *B. schneideri* the smallest viperid (Greene, 1997; Branch, 1998). Additionally, the species is currently classified as Vulnerable by the IUCN (World Conservation Monitoring Centre, 1996). Accordingly, information regarding the biology of this species can inform studies of broad-scale ecological and evolutionary questions regarding other small arid-adapted viperids, as well as conservation-oriented management decisions.

We quantified body size, size-class distribution, morphology, sexual size dimorphism (SSD), and growth rates for a population of free ranging *B. schneideri*. We used these measures to evaluate various candidate selective pressures that may have been responsible for the evolution of small body size in this species.

Sexual dimorphism in snakes has been widely investigated and reviewed (Shine, 1978, 1990, 1993, 1994; Fitch, 1981; Bonnet et al., 1998). These reviews have made several inferences about the effects of overall body size on morphological traits and SSD (Shine, 1993). Shine (1993) and Madsen and Shine (1994) suggest that females of smaller species are likely to be larger than conspecific males. Conversely, Shine (1993) suggests that males are likely to be larger than conspecific females in species where male-male combat is common.

Although *B. schneideri* is reported to exhibit sexual dimorphism in tail length (Broadley, 1983; Branch, 1998; Shine et al., 1998) and the degree of sub-caudal scale keeling (Shine, 1993; Branch, 1998), these conclusions are based on very few data from *B. schneideri* and inference from trends recorded for closely related species.

Previous research on SSD for other species of snakes provides a basis for predictions regarding SSD in *B. schneideri* morphology. (1) We expected female *B. schneideri* to be longer than males. Female snakes are generally larger than males, particularly in smaller (Shine, 1978; Fitch, 1981; Shine, 1993; Shine, 1994) and viviparous species (Fitch, 1981; though see Shine, 1993). Our observations suggest that *B. schneideri* do not exhibit male-male combat (see Shine, 1978). (2) Females should also be heavier than males because

females are heavier bodied than males in most species including the closely related *B. caudalis* (Shine, 1994; Shine et al., 1998). (3) We expected males to have longer tails than females of the same body length (Fitch, 1981; King, 1989), and female snakes to have relatively larger heads than male snakes as observed in other species (Shine ,1994). (4) Given that sexual differences in head size and shape are common to snakes (Shine, 1986; Shine, 1993), we expected to find differences between the sexes for head characteristics with females having broader heads.

Additionally, the small body size of *B. schneideri* individuals suggests a relatively short life-span. Accordingly, we predicted that individual *B. schneideri* should exhibit rapid growth as early maturation would be selected for in order to maximize life-time reproductive output (Madsen & Shine, 1992).

2.2 Materials and Methods

2.2.1 Study site

We studied a population of *B. schneideri* on the farm Noup on the Namaqualand Coast, Northern Cape Province, South Africa (30°08′ S; 17°12′ E). The region receives approximately 50 - 150 mm of rain per annum, but condensation of coastal fog represents a major input of water to this ecosystem (Cowling et al., 1999; Desmet, 2007). In general, temperatures are determined by wind direction, with dominant southerly winds significantly cooling day-time temperatures, and easterly winds producing hot, dry conditions. Summer temperatures are mild (mean = 18.2 ºC), while winter temperatures are cool (mean = 14.3 ºC; Desmet, 2007). *Bitis schneideri* inhabits semi-vegetated, ocean-derived, aeolian sand deposits of varying depth. Vegetation structure and botanical composition are relatively homogenous across the habitat in which the snakes occur. Abundant plant species that significantly contribute to vegetation structure include *Lycium cinereum*, *Zygophylum morgsana*, *Lebeckia sericea*, *Ruschia robusta*, and *Cladoraphis cyperoides*.

2.2.2 Measurements and analysis

We actively searched for individual *B. schneideri* over a period of 16 months during three consecutive austral summers between September 2007 and March 2010. On most days, searching lasted between two and five hours (mean = 2.8 hours.day^{-1}). We captured 101 female, 124 male, and 60 juvenile (SVL < 140 mm) individuals, totalling 285 captures. All

snakes were uniquely marked by ventral scale clipping. We measured SVL, tail length, and mass of each snake. SVL and tail length were measured by placing the anterior portion of the snake into a transparent acrylic tube, and measured using a ruler. Each snake was weighed to the nearest 0.1 g using a digital field balance. Additionally, a subsample of 54 individuals were digitally photographed while resting on graph paper and appropriately scaled in ImageJ (Abramoff et al., 2004). From this subsample we measured head length (HL - straight line distance from the angle of the jaw to the tip of the snout) and head width (HW - straight line distance across the widest part of the head). We also calculated two secondary head metrics: head area (HA: product of HW and HL) as an index of overall head size, and head shape (Shape: division of HL by HW) as an index of head shape: large values suggest longer heads, small values suggest wider heads.

The degree of sexual dimorphism for each trait was calculated by dividing the mean value from the larger sex by the mean value from the smaller sex (Gibbons & Lovich, 1990). The index for degree of sexual dimorphism was arbitrarily designated as positive when favouring females. We compared adult SVL between males and females using a one-way T-test with SVL as dependent variable and sex as the categorical predictor. Comparisons of head characteristics relative to body length were made among adult males and females using analysis of covariance (ANCOVA). Comparisons of mass and tail length were made relative to body length and compared among adult males and adult females using ANCOVA.

We also examined 22 road-killed individuals (13 males, 9 females) for the presence and extent of keeling on subcaudal scales as described in the literature (Haacke, 1975; Shine, 1993; Branch, 1998). All analyses were performed in Statistica v. 6 (Statsoft, 2001). Results were considered statistically significant for $p < 0.05$.

We used growth data collected from 26 recaptured snakes (14 females, 12 males) to estimate growth rates. We calculated the parameter *K*, which defines the shape of the Von Bertalanffy growth function, using a Standard Forced Gulland and Holt Plot (De Graaf & Prein, 2005). The Von Bertalanffy growth function is known to fit growth patterns in snakes accurately and has been frequently used in the literature for this purpose (Andrews, 1982; Plummer, 1985; Webb et al., 2002a; Webb et al., 2003). We chose an asymptotic length of 264 mm for our calculations as this value was 5% longer than the longest individual measured during our study (Taylor, 1962; Pauly, 1981; Shine & Chanov, 1992).

2.3 Results

Snout-vent length measured from 285 wild-caught individuals ranged from 96 mm to 251 mm and mean ± SD adult SVL (individuals with SVL > 140 mm) was 198.7 ± 25.0 mm (Fig. 2.1). Body mass ranged from 2.5 g to 35.5 g and mean ± SD adult mass was 15.8 ± 6.3 g (Fig. 2.2). Length and mass did not regress linearly, with adult snakes (particularly females) becoming disproportionately heavier as they gained in length (Fig. 2.3).

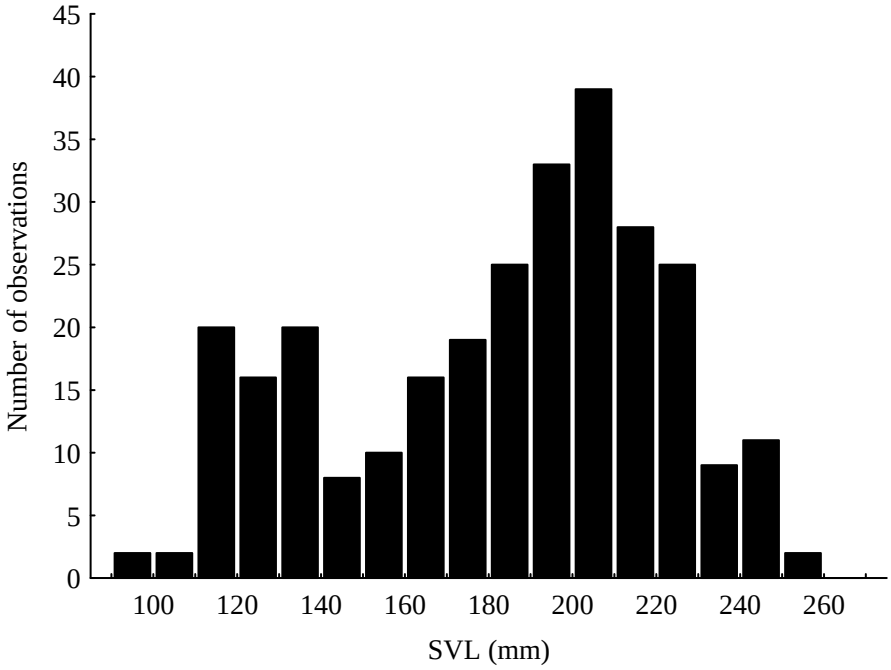


Figure 2.1: Length-class distribution for 285 *Bitis schneideri* measured during our study, over three austral summers between September 2007 and March 2010.

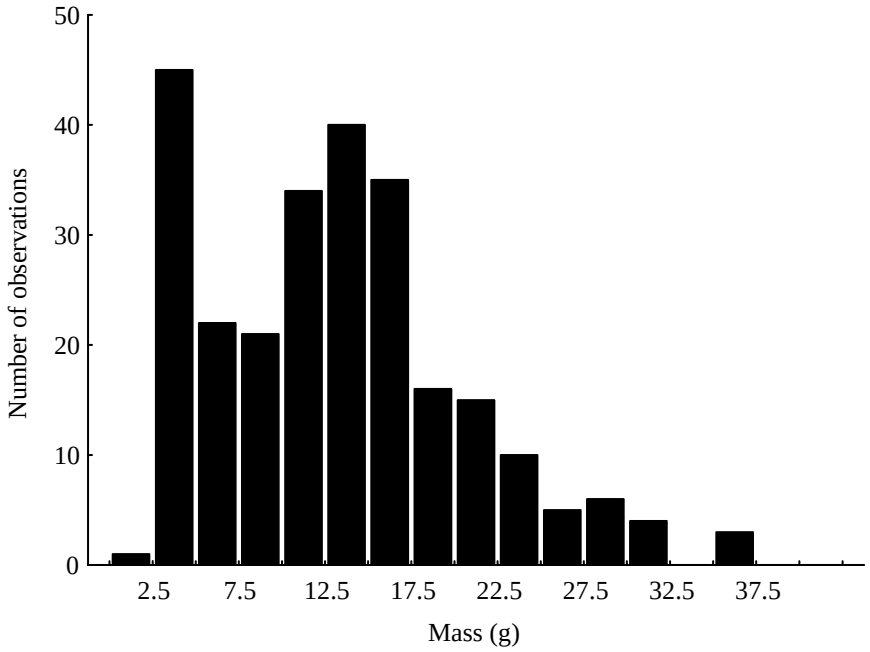


Figure 2.2: Mass-class distribution for 257 *Bitis schneideri* measured during our study, over three austral summers between September 2007 and March 2010.

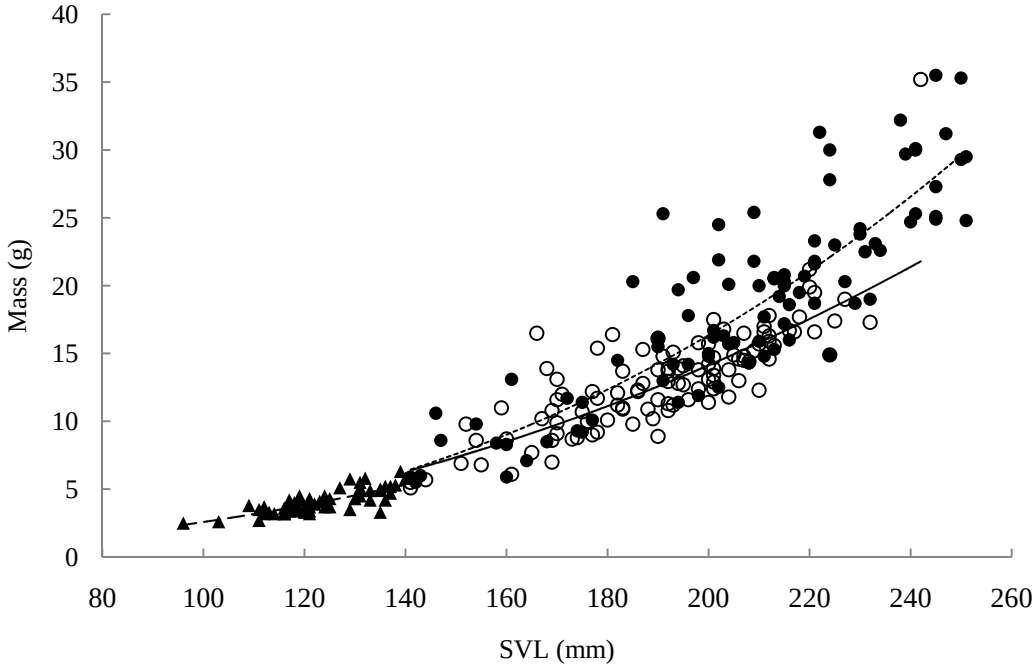


Figure 2.3: The relationship between mass (g) and SVL (mm) for 56 juvenile (▲), 92 adult female (●), and 109 adult male (○) *Bitis schneideri.* Fitted lines represent power relationships for juvenile (Mass = 0.0001 x SVL2.16), adult female (Mass = 0.00001 x SVL2.67), and adult male (Mass = 0.00008 x SVL$^{2.27}$) *Bitis schneideri*.

Predictions regarding sexual size dimorphism in *B. schneideri* were supported in all cases (Table 2.1). Mean ± SD adult SVL was greater in females (207.4 ± 27.6 mm) than males (191.6 ± 20.2 mm; ANOVA: $F_{1, 223} = 24.37$; $P < 0.001$). Analysis of covariance indicated that the slopes of the regressions of tail length on SVL in each sex were parallel, and that tail length was longer in males than females of the same body length (ANCOVA: $F_{1,222} = 287.78$; $P < 0.001$, Fig. 2.4). The slopes of the regressions of mass on SVL in each of the sexes were not parallel, precluding us from reporting the main effects of the ANCOVA. However, the differences in slopes (females: m = 0.22; males: m = 0.15) showed that female snakes were heavier than males of the same body length. The slopes of the regressions of each of the head metrics (HL, HW, HA, and HS) on SVL in each sex were parallel. Differences in head length (ANCOVA: $F_{1, 35} = 3.70$; $P = 0.063$) and head width (ANCOVA: $F_{1, 35} = 3.54$; $P = 0.068$) were not statistically significant, but head area was significantly greater in females than males of the same length (ANCOVA: $F_{1, 35} = 6.13$; $P = 0.018$). Head length and head width increase proportionally (Pearson's $R = 0.94$) indicating that head shape changes little with increasing size. Head shape did not vary among sexes (ANCOVA: $F_{1, 35} = 0.00$; $P \approx 1.00$).

Table 2.1: Mean measures of morphological traits (mean ± SD (N)), degree of SSD (Gibbons and Lovich, 1990; positive for females, negative for males), and statistical test of significance for *Bitis schneideri*.

Adult Trait	Males	Females	Degree of SSD	P
SVL (mm)	191.63 ± 20.25 (124)	207.40 ± 27.60 (101)	+ 1.08	<0.001***
TL (mm)	24.35 ± 3.54 (124)	19.12 ± 3.37 (101)	- 1.27	<0.001***
HW (mm)	13.85 ± 1.32 (16)	14.98 ± 1.73 (22)	+ 1.08	0.068
HL (mm)	16.51 ± 1.35 (16)	17.66 ± 1.63 (22)	+ 1.07	0.063
HA (mm^2)	230.08 ± 39.88 (16)	266.79 ± 50.14 (22)	+ 1.16	0.018*

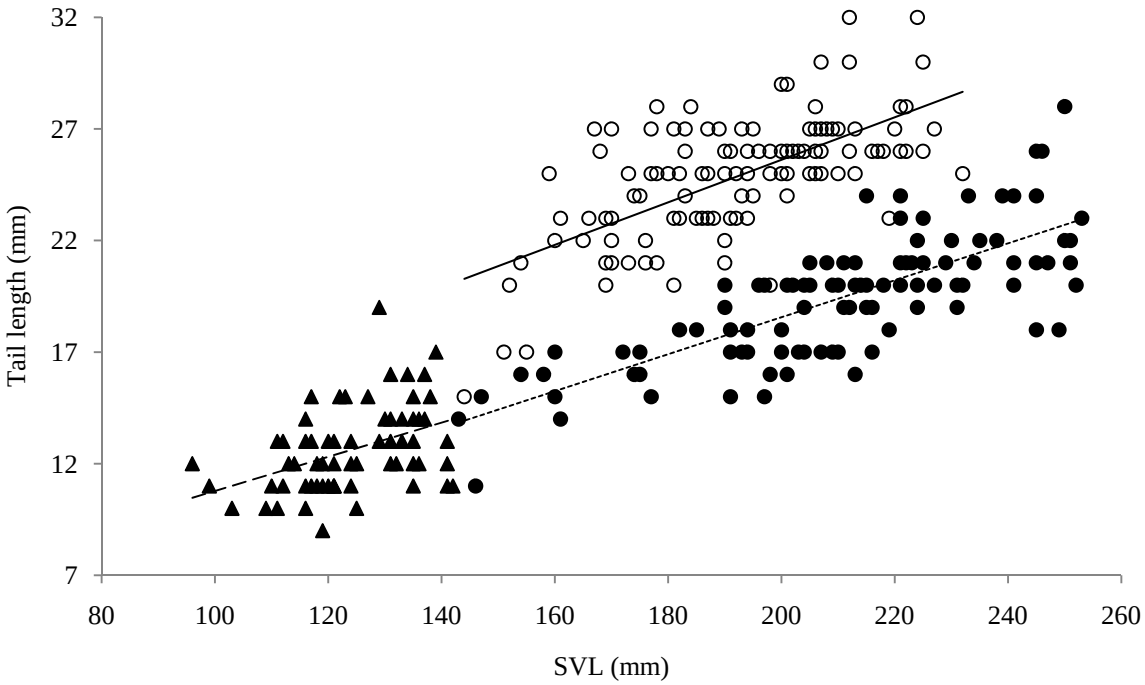


Figure 2.4: The relationship between SVL (mm) and Tail length (mm) and for 64 juvenile (▲), 103 adult female (●), and 120 adult male (○) *Bitis schneideri*. Fitted lines represent straight lines regressions for juvenile (TL = 0.076.SVL + 3.12), adult female (TL = 0.083.SVL + 2.00), and adult male (TL = 0.095.SVL + 6.57) *Bitis schneideri*.

Examination of the preserved specimens confirmed that subcaudal keeling is more extensive in females than males. Subcaudal scales of females are keeled along the length of the tail while those of males are keeled along the posterior half only.

Growth rate is size dependent and decreases with increasing SVL (Pearson's R = -0.69). We detected no sex effects on growth rate (ANCOVA: $F_{1, 20} = 0.97$, $p = 0.34$), though this may have resulted from the poor statistical power resulting from small sample size. The slope of the regression of dSVL/dT against asymptotic length minus mean SVL (Fig. 2.5) yielded an estimated $K = 0.0012$ day^{-1} or 0.438 year^{-1}. The predicted theoretical growth trajectory showed that, on average, snakes reach mean adult body length of approximately 200 mm at approximately 2.2 years of age (Fig. 2.6).

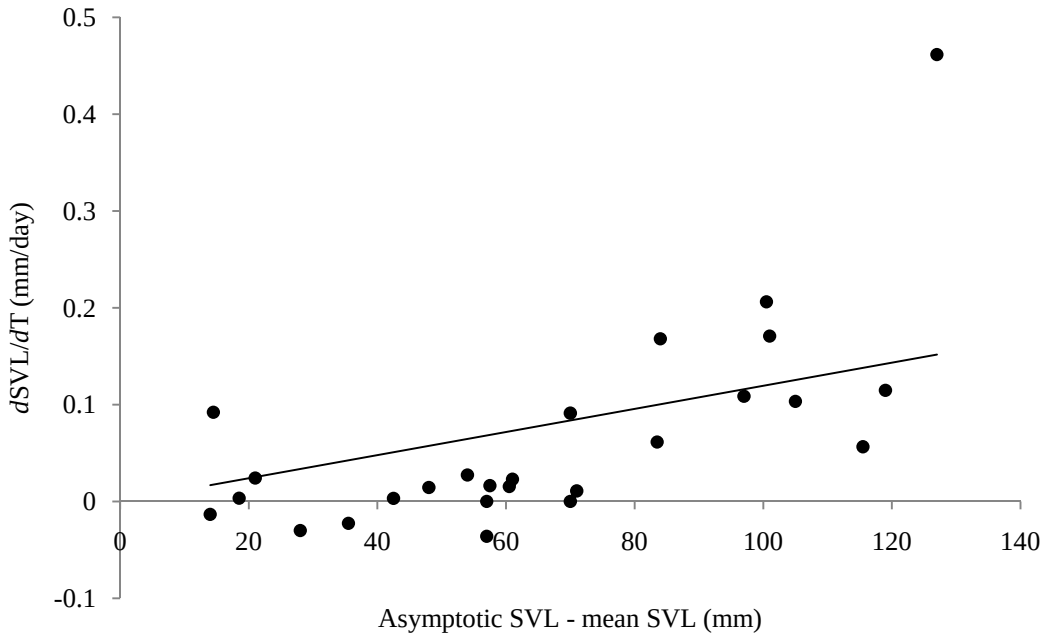


Figure 2.5: Standard Forced Gulland and Holt plot, showing change in growth rate with SVL. The slope of the regression line forced through the origin (0.0012 day^{-1}) and represents the parameter K in the Von Bertalanffy growth function.

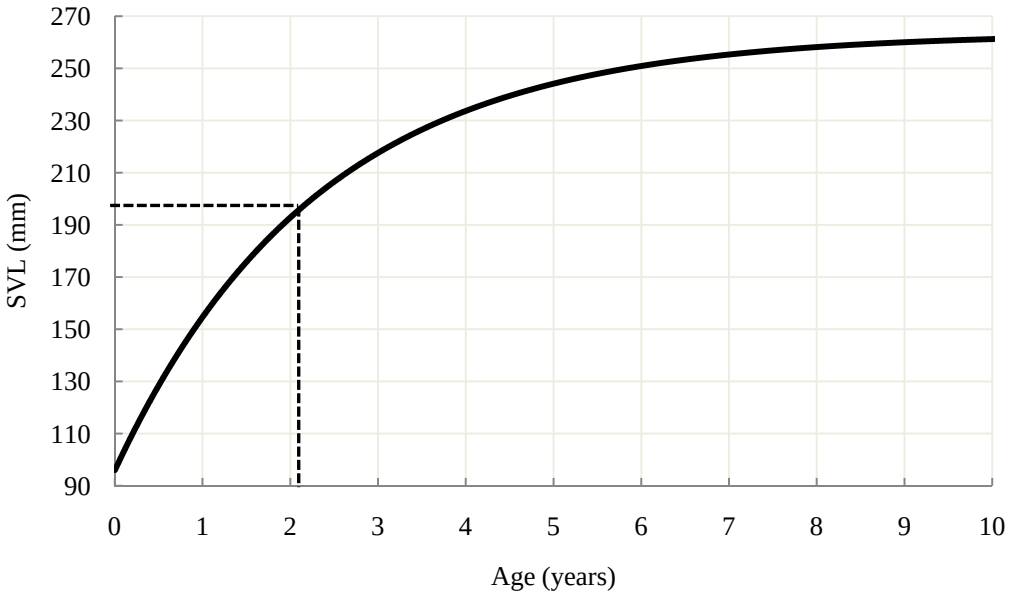


Figure 2.6: Standard Forced Gulland and Holt plot, showing change in growth rate with SVL. The slope of the regression line forced through the origin (0.0012 day^{-1}) and represents the parameter K in the Von Bertalanffy growth function.

2.4 Discussion

2.4.1 Body size

Our data confirmed that *B. schneideri* is the smallest viperid, with maximum length not likely to significantly exceed 254 mm, and body mass not exceeding 38 g. Small body size in this species may be the result of several selective pressures, which may not be mutually exclusive.

Firstly, several studies have demonstrated that shifts in body size (in both directions) of insular snake populations can be attributed to variations in the size of available prey items (Boback, 2003; Keogh et al., 2005). Small body size in *B. schneideri* may also have been driven by this selective pressure. Field observations at our study site suggest that there is a gap in prey size distributions (small reptilian and amphibian prey items are common, but the dominant rodent *Otomys unisulcatus* is relatively large (100 - 150 g), smaller rodent species are rare, and there are few prey items between 15 g and 100 g). Thus the small body size of *B. schneideri* could be the result of a shift towards the smaller body size of prey species. It is important to note that within the *B. caudalis* complex, mean adult body size appears to increase with increasing aridity (Shine et al., 1998).

Secondly, the scarcity of prey in arid environments has also been postulated to have resulted in a dietary shift in *Echis* from vertebrate to invertebrates, often to an extreme degree (e.g., *Echis coloratus* and *E. pyramidium*; Barlow et al., 2009). Our observations have not detected any such shifts in the diet of *B. schneideri.* It is therefore possible that a reduction in body size may represent an alternative solution to the problem of reduced food availability.

We propose an alternative hypothesis for the evolution of small body size in *B. schneideri*: small body size provides physiological and ecological advantages when burying into sandy substrates. The ability of a snake to bury its body just below the surface of the sand substrate, as *B. schneideri* does, has evolved independently on several occasions in arid adapted viperids, often with morphological correlates (the placement of the eyes of *Bitis peringueyi* and *Cerastes vipera*; ocular decorations such as *Bitis caudalis*, *Cerastes cerates* and *C. gasperetti*). This capacity appears to also be correlated to small body size: *Bitis schneideri* and *B. peringeuyi* are the two smallest species within the genus, *Cerastes vipera* is smaller than its congeners, *Eristocophis macmahoni* is generally smaller than closely related *Pseudocerastes* spp., and *Crotalus cerastes* is small relative to most of its congeners. Within the morphologically similar elapid genus *Acanthophis*, *A. pyrrhus* is smaller than *A.*

antarticus or *A. praelongus*. We suggest that large body size may hinder the effective use of this microhabitat in two ways. Firstly, large snakes have difficulty in burrowing into densely-packed aeolian sand, due to mechanical constraints. Secondly, the range in sub-surface soil temperatures decreases very rapidly with depth (Campbell & Norman, 1998), effectively prohibiting large, thick-body snakes from achieving target temperatures as the ventral body parts would be in contact with cold sand throughout the diel cycle.

Near to the surface, the subsurface thermal profile provides a favourable microclimate for an *B. schneideri*: it is warmed by incident radiation during the day, allowing small snakes to warm to target temperatures without being exposed, and provides a buffered thermal environment that can maintain heat loads into the evening when air temperatures decrease. Thus, small bodied snakes can easily and effectively thermoregulate while remaining hidden by burying below the surface. Remaining buried in the sand is also an ideal ambush position.

2.4.2 Sexual dimorphism

We found that female *B. schneideri* are larger and more heavy-bodied than males. Females also have larger heads but males have long tails. These sexually dimorphic trends are common among snakes and have generally been attributed to three suites of selective pressures: sexual selection, natural selection, and fecundity selection (Shine, 1993). Unfortunately, teasing apart the determinants of sexually dimorphic traits is difficult (Katsikaros & Shine, 1997). While our study has highlighted various sexually dimorphic traits in *B. schneideri*, our data do not allow us to confidently attribute causality to these traits. However, given that sexual dimorphism in *B. schneideri* appears to fit trends from other studies, we agree with the standing hypotheses proposed for other snake species.

Females of many species of snakes are relatively longer and heavier-bodied than conspecific males (Fitch, 1981; Shine, 1993; Shine et al., 1998). This difference is likely a result of fecundity selection, whereby larger females tend to produce larger clutches (Semlitch & Gibbons, 1982). This selection is especially important in small species where reproductive output is limited by body-size constraints (e.g., Hedges, 2008) and is likely the selective pressure that has maintained sexual dimorphism in body size in *B. schneideri*.

Sex differences in tail length (relative to SVL) are common in snakes, particularly among lineages with relatively short tails (King, 1989; Shine, 1993). King (1989) suggests three alternative hypotheses regarding the evolution of sexual dimorphism in tail length. Two of

these, fecundity selection for a more posterior placement of the cloaca in females, and morphological constraint of housing the hemipenes and associated musculature in males, are relatively well supported by King's review of colubrid snake morphology. The third hypothesis, that increased tail length in males is a result of a mating advantage during courtship, is unlikely to be important in snakes with relatively short tails such as *B. schneideri*, and where male combat does not appear to occur. King (1989) also demonstrated that the hemipenes and associated musculature make up a greater proportion of the tail volume in species with relatively short tails. It is possible that morphological constraint has resulted in the evolution of longer and thicker tails in male individuals.

Changes in tail morphology of males appear to be associated with maturity, with juvenile tail morphology exhibiting similar traits to females (Fig. 2.4). Tail length in males appears to increase rapidly at body lengths approximating maturity. This suggests that increased growth at the base of the tail to house the hemipenes only takes place at maturation. Since these tissues have a different temporal (and possibly spatial) origin, it may explain the lack of subcaudal keeling in the anterior part of the male tail.

Differences in head size relative to body length were also expected (Shine, 1993). Shine (1991) reviewed head size dimorphism in snakes and found that 47% of the 114 species examined showed sexual dimorphism in head length. Generally such differences are interpreted as the result of differences in diets between the sexes (Shine, 1991), although this need not always be the case. Shine and Crews (1988) demonstrated that differences in head size among male and female Red-sided Garter Snakes (*Thamnophis sirtalis parietalis*) resulted from changes in growth associated with gonadal hormone secretion. Thus differences in head size among sexes may result from changes in hormonal production resulting from some other cause and may not necessarily be functionally related to diet specialization.

We were unable to test for differences in diet among sexes due primarily to the infrequent feeding occasions for which we have data. Ecological differences in prey size (or prey size range) would provide interesting insight into the ecology of *B. schneideri*. An analysis of the gut content of museum preserved *Bitis caudalis* showed that female snakes were more likely to feed on mammalian prey (Shine et al., 1998). It is possible that *B. schneideri* females share this propensity because of the ecological similarities and phylogenetic proximity between the two species.

Sex differences in relative head size have been detected among juveniles of some species (King et al., 1999), though we were unable to test for this trend among juveniles because of the difficulties involved with sexing juvenile snakes and the relatively small number of neonate snakes that we captured.

2.4.3 Growth

Our growth data suggests that individual *B. schneideri* grow very rapidly and are likely to reach mean adult body length (≈ 200 mm) at approximately 2.2 years of age. This finding is supported by the bimodal distribution of body lengths (Fig. 2.1). This pattern can easily be explained by rapid growth if data were collected only during one season. Our estimated value for *K* (0.438 $year^{-1}$) was similar to other estimates of *K* for other snake species in the literature (Shine & Charnov, 1992; Webb et al., 2003). Webb et al. (2002a) demonstrated that *Acanthophis praelongus* from tropical Australia grows rapidly and matures quickly despite the ecological expectations resulting from the study of congeners (Shine, 1980) and other ambush predators (Webb & Shine, 1998). Unfortunately we do not have direct data on age at maturity in *B. schneideri*. However, Andrews (1982) demonstrated strong allometric relationships between mean adult SVL and SVL at maturity for snakes. This allometric relationship suggests that males and females *B. schneideri* should reach sexual maturity at approximately 150 mm and 170 mm SVL respectively. Our growth data suggest that males and females are reaching these reproductive lengths at approximately ten and 15 months respectively. These estimates are much shorter than those for other viperid species. Shine (1980) reports mean age of maturation for females of eight species to be 44.3 months. Our data also suggest that males are likely to be sexually mature by one year of age and could breed during the first mating season of their lives. Since large snakes tend to be longer-lived than small snakes, and larger species tend to have larger reproductive output (Dunham & Miles, 1985), we propose that *B. schneideri* has evolved rapid growth as a mechanism of increasing total lifetime reproductive output.

Our data suggest that *B. schneideri* is very small snake that exhibits typical sexual dimorphic traits that have probably been shaped by the same selective pressures that are acting on other snake species. Our data also suggest that *B. schneideri* exhibits very rapid growth and that such rapid growth has evolved in order to maximize total life time reproductive output, in the face of size constraints. Future studies into the biology and evolution of *B. schneideri* and

other southern African snakes have the potential to provide a valuable contrast to the northern-temperate dominated literature regarding snake biology (Cottone & Bauer, 2009).

2.5 Acknowledgements

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CHAPTER 3

SEASONAL VARIATION IN MOVEMENT PATTERNS OF AN ARID-ADAPTED VIPER FROM SOUTHERN AFRICA

Abstract – The timing of bouts of movement by an organism is important as it affects benefits and costs during phases of movement. We investigated variation in the timing of movement in a population of Namaqua Dwarf Adders (*Bitis schneideri*) using radio telemetry and field observations. We measured the proportion of individuals that were moving at different times of the day, at different times of the year, and relative differences between sexes. We also assessed the degree to which environmental variables (air temperature, relative humidity, atmospheric pressure, and wind speed) varied among encounters with moving and non-moving snakes. Telemetry data showed that snakes were more likely to move during the day-light hours, with a peak in movement during the late afternoon. Our field observations revealed that Namaqua Dwarf Adders show seasonal variation in movement, moving more frequently during spring months than during other seasons. This finding was supported by data from telemetered snakes that showed that snakes move between 93% and 30% of days depending on their sex and the season. Principal component analysis showed that movement was linked more closely to environmental conditions during winter, than in summer or spring. Our data also show that environmental conditions had a far greater influence on movement during winter, when conditions were generally less suitable for movement. We hypothesise that the observed variation in movement patterns at all temporal scales is the result of the selective pressure imposed by the costs of activity during sub-optimal environmental conditions.

3.1 Introduction

Movement (displacement from one location to another) has important implications for organisms and is necessary for most aspects of their biology (Nathan, 2008). As a result, studies of the timing of bouts of movement help elucidate the ecological pressures experienced by organisms (Bonnet et al., 1999) and the evolutionary history of the species

(Luiselli, 2001). This information is also essential for understanding the life-history and ecology of organisms, and thus developing adequate conservation and management plans (Dodd et al., 2004). Yet despite its importance, few studies (Alexander, 1997; Alexander & Marshall, 1998) have measured the timing of bouts of movement in African snakes.

The decision to move represents the trade-off between the advantages of moving at a particular time, and the cost associated with that movement (Metcalf et al., 1999). Thus, it is not surprising that many organisms vary the timing of bouts of movement to maximise the associated benefits and minimise costs. For example, many organisms limit foraging activity to night-time hours to reduce the risk of predation from diurnal predators (Metcalf et al., 1999), while others avoid heat stress and risk of desiccation during the hottest hours of the day by moving at night (Walsberg, 2000).

For many organisms, environmental conditions can constrain the timing of movement. In extreme cases, environmental conditions may limit phases of movement to a few months in the year. At broad temporal-scales variation in the timing of bouts of movement are observed as seasonality, while variation at short temporal-scales is conventionally classified as nocturnality, diurnality or crepuscularity. Assessment of variation in observed patterns reveals the interplay of factors influencing movement and the mechanisms that result in the observed patterns. This provides a framework for understanding other aspects of ecology and evolution, which, in turn, allows for the development of effective conservation management.

We investigated the patterns of movement of a small, arid-adapted viperid from southern Africa, *Bitis schneideri*. Because *B. schneideri* is an ambush predator, quantifying the degree to which resting time and foraging time is partitioned is impossible (resting positions and ambush positions are indistinguishable). We therefore investigated the timing and frequency of movement, rather than activity patterns in general. Specifically we aimed to investigate 1) what time of day *B. schneideri* individuals are most likely to move, 2) whether *B. schneideri* exhibits seasonal or sexual variation in the frequency of movement, and 3) to what degree are patterns of movement related to environmental conditions and food availability. In accordance with the ecology of most temperate environment snake species, we predict that patterns of movement will show seasonal variation associated with environmental suitability, as well as sex-based differences associated with mating behaviours.

Given the biological uniqueness and general lack of faunal ecological understanding of the Succulent Karoo Biome to which *B. schneideri* is endemic, as well as the conservation concerns regarding the species, our results have important implications for understanding and managing arid-adapted species in the region.

3.2 Methods

3.2.1 Study animal

Bitis schneideri is the smallest viper. It is arid-adapted and inhabits coastal dune systems along the southern Africa west coast (Broadley, 1983; Branch, 1998). Although it is currently listed as Vulnerable by the IUCN (Branch, 1988; World Conservation Monitoring Centre, 1996), recent evaluations suggest that its conservation status is likely to change to Least Concern in the future. Like most other viperids, *B. schneideri* is an ambush predator and individuals thus tend to be relatively sedentary compared to actively-foraging species. Although it is not known which factors influence movement, risk of avian predation may be important (Maritz & Scott, 2010).

3.2.2 Study site

Our study site falls within the Succulent Karoo Biome (Mucina & Rutherford, 2006) of southern Africa, one of two globally-recognised, arid biodiversity hotspots (Myers et al., 2000). All investigations took place on the farm Noup (30° 08’ S; 17° 12’ E), Northern Cape Province, South Africa. The study site receives less than 150 mm rainfall per annum, but coastal fog is frequent (Cowling et al., 1999). More than 60% of the annual rain falls during winter (Desmet, 2007). Temperatures are cool, ranging from a mean temperature of 14.3 °C in winter to 18.2 °C in summer (Desmet, 2007). The habitat in the area is relatively homogeneous and consists primarily of semi-vegetated, longitudinal aeolian dunes, dominated by sclerophyllous shrubs and succulents (Mucina & Rutherford, 2006).

We collected data on the timing of movement by Namaqua Dwarf Adders using two approaches. We used data collected from 585 hours of active searching for snakes, and supplemented these with data collected from 37 snakes fitted with miniature radio-frequency transmitters.

3.2.3 Field surveys

We surveyed (active searching by at least one experienced observer, for at least one hour) the study site on 350 occasions, between October 2007 and July 2010, in search of Namaqua Dwarf Adders. Survey effort was biased toward warmer months: September (37 surveys), October (43 surveys), November (65 surveys), December (45 surveys), January (23 surveys), February (45 surveys), and March (52 surveys). However, we were also able to conduct surveys during the months of April (4 surveys), May (1 survey), June (20 surveys), and July (15 surveys). No surveys were conducted during August. Surveys were conducted at various times throughout the day, but primarily during the morning (generally between 08:00 and 11:00) and afternoon (generally between 15:00 and 19:00) when the ambient lighting conditions were best for detecting snake tracks. The tracks left by Namaqua Dwarf Adders are unique and are easily differentiated from other syntopic snake species.

During each survey we recorded the number of observers, the duration of the survey, and the number of snake tracks observed during each survey. Since wind speed was likely to influence the persistence of tracks, we also recorded wind speed at the start of each survey using a Kestrel 4000 hand-held weather meter (Kestrelmeters.com). Whenever a snake was encountered we recorded the time of day and the behaviour (moving, resting/ambush) being exhibited. We also recorded the shaded air temperature at ground level (°C), wind speed approximately 1 m above the ground ($m.s^{-1}$), relative humidity (%), and atmospheric pressure (hPa) using a Kestrel 4000 hand-held weather meter.

3.2.4 Radio telemetry

We actively searched for and captured 37 adult *B. schneideri* from the study site for radio telemetry work. Transmitters (BD-2NT, Holohil Systems Limited) were attached using a cyanoacrylate adhesive to the dorsal surface of the snakes slightly anterior to the tail, so that the 140 mm whip antenna trailed behind the snake. We used small, lightweight transmitters (0.55 g) because of the small body size of *B. schneideri* (mean adult snout-vent length = 200 mm; Maritz & Alexander, In Press-a) and thus were limited to short battery lives (21 days at 40 °C; according to manufacturer specifications). Accordingly, telemetry work was limited to three sessions during spring (October 2009), summer (December 2008 - January 2009), and winter (July 2010; see Maritz & Alexander, Submitted). All telemetered snakes were released at point of capture within seven days of capture. Each snake was located daily using a

Communications Specialist R1000 handheld receiver and 3-element Yagi antenna. During each encounter we recorded the time of day and the behaviour (moving, resting/ambush) exhibited by the snake. We also recorded the location of each snake using a handheld GPS (Garmin *eTrex*; Datum WGS 1984), and marked each location with orange flagging tape. Finally we measured shaded air temperature at ground level (°C), wind speed approximately 1 m above the ground ($m.s^{-1}$), relative humidity (%), and atmospheric pressure (hPa) using a Kestrel 4000 hand-held weather meter.

3.2.5 What time of day does B. schneideri *move?*

For logistic reasons, our field observations were primarily limited to day-time hours. However, night-time searches never revealed active snakes, and only once did we incidentally locate an active individual at night (a male during spring). Conversely, 10.7 % of all radio-telemetry observations during day-time hours were of active snakes. Moreover, our study site frequently receives strong winds during afternoon hours, but still evenings. On mornings following such conditions, we rarely encountered snake tracks. These observations strongly suggest that Namaqua Dwarf Adders are more likely to move during day-time hours. In order to assess variation of activity within day-time hours, we plotted the proportion of snakes that were active during observations made of snakes fitted with radio transmitters. Visual inspection of these data suggested little variation in the timing in movement between seasons. We therefore pooled the data for all seasons in order to estimate overall variation in diel activity.

3.2.6 Does B. schneideri *exhibit seasonal variation in movement?*

To assess the relative amount of movement in each season we compared the relative number of tracks observed ($tracks.observers^{-1}.hour^{-1}$) during field surveys. We pooled the data into four three-month seasons (spring – September to November, summer – December to February, autumn – March to May, and winter – June to August) and compared track abundance during each season using analysis of covariance with wind speed included as a covariate. Additionally we calculated the proportion of observations of telemetered snakes that were active when observed, and compared these across each of the three telemetry seasons using χ^2 analysis.

3.2.7 Does B. schneideri *exhibit sexual variation in frequency of movement?*

We calculated the proportion of days during which telemetered individuals moved (total number of days with movement of more than 2 m divided by the total number of days of observation), during each telemetry session and compared this measure (after arcsine transformation) between sexes and seasons using factorial analysis of variance.

3.2.8 To what degree are patterns of movement related to environmental conditions and prey availability?

We investigated the degree to which environmental variables influenced movement patterns separately for each season using Principal Components Analysis (PCA) to distil the four measured and auto-correlated environmental variables down to two principal components (PC1 and PC2). We then compared mean principal component vector for telemetered individuals that were active or not active when observed using Student's T-test. Additionally, we correlated mean estimated prey encounter rates (see Chapter 7) with a proxy for snake movement (track abundance) to investigate the degree to which movement is correlated with prey availability.

3.3 Results

3.3.1 What time of day does B. schneideri move?

The likelihood of a Namaqua Dwarf Adder being active was not even through the day (χ^2 = 895.33, $p < 0.001$; Fig. 3.1). The proportion of Dwarf Adders active during telemetry observations was generally low (8%). Although limited by sample size, observations during the middle of the day suggest that snakes may move less frequently during the hottest part of the day.

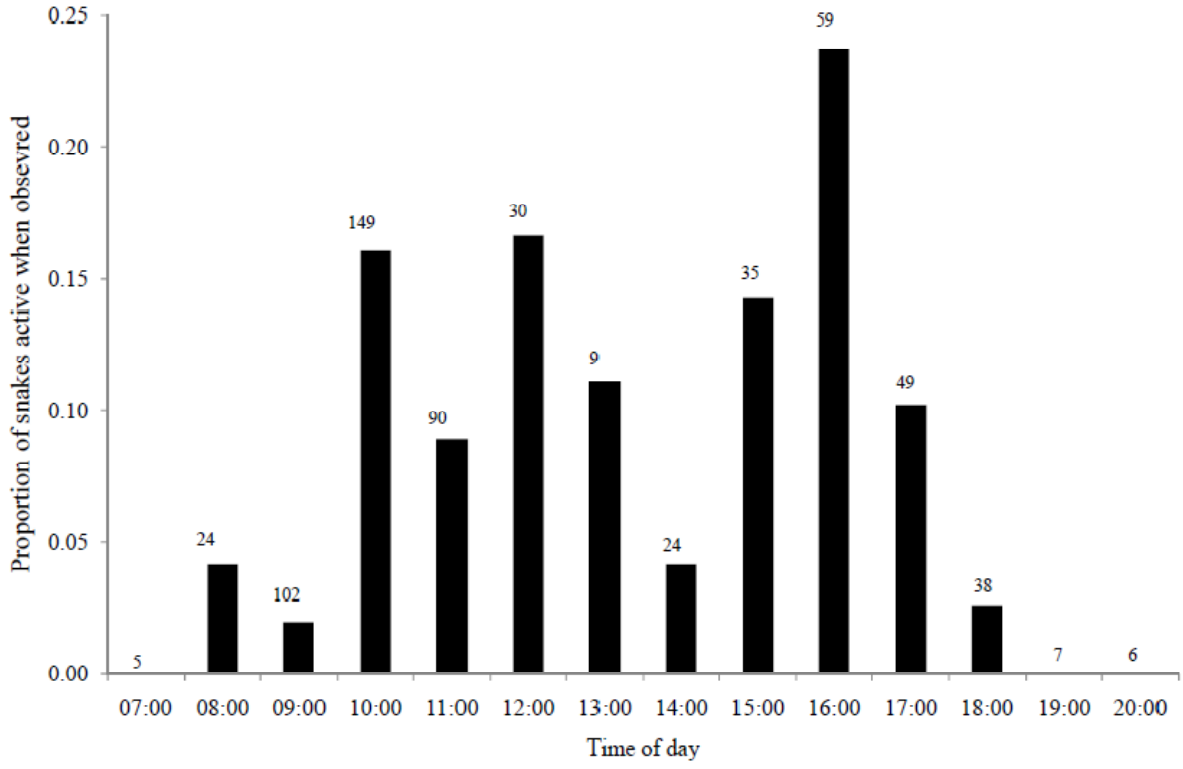


Figure 3.1: Proportion of telemetered snakes that were moving when observed at different times of the day.

3.3.2 Does B. schneideri exhibit seasonal variation in movement?

Our analysis of the prevalence of Namaqua Dwarf Adder tracks varied significantly across seasons (ANCOVA: $F_{(3,345)} = 22.69$, $p < 0.0001$, Fig. 3.2). Tukey HSD test for significant differences showed higher levels of movement during spring. Observations of radio-tracked snakes over three seasons mirrored these findings: During spring, snakes were more likely to be active when observed (22%), than during summer (6%) or winter (7%; $\chi^2 = 13.77$, $p < 0.001$).

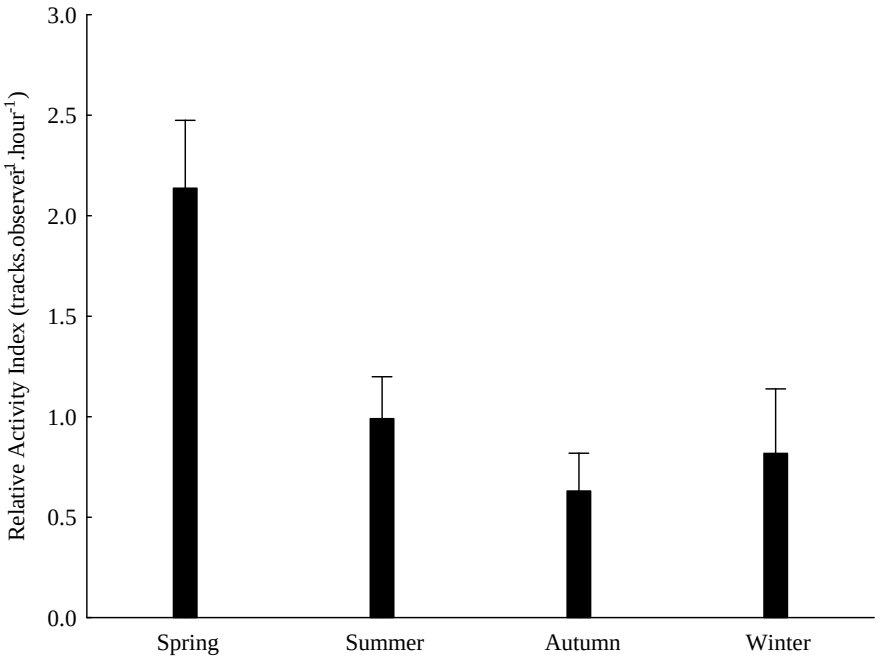


Figure 3.2: Relative Activity Index showing weighted mean seasonal activity levels estimated from the encounter of tracks. Tukey HSD test for significant differences shows that activity in spring (September, October, and November) is significantly higher than all other seasons.

3.3.3 Does B. schneideri exhibit sexual variation in frequency of movement?

The proportion of days during which male and female snakes moved varied significantly across seasons and sexes (ANOVA: $F_{(2,31)} = 5.26$, $p = 0.01$, Fig. 3.3). Tukey HSD post-hoc analysis revealed that during spring, males (93.1 ± 4.8% of days) moved significantly more often than females (64.9 ± 5.6%). However, there were no significant differences between males and females in summer (males 67.1 ± 5.6%; females 66.5 ± 4.5%) or winter (males 50.9 ± 6.1%; females 29.0 ± 7.9%).

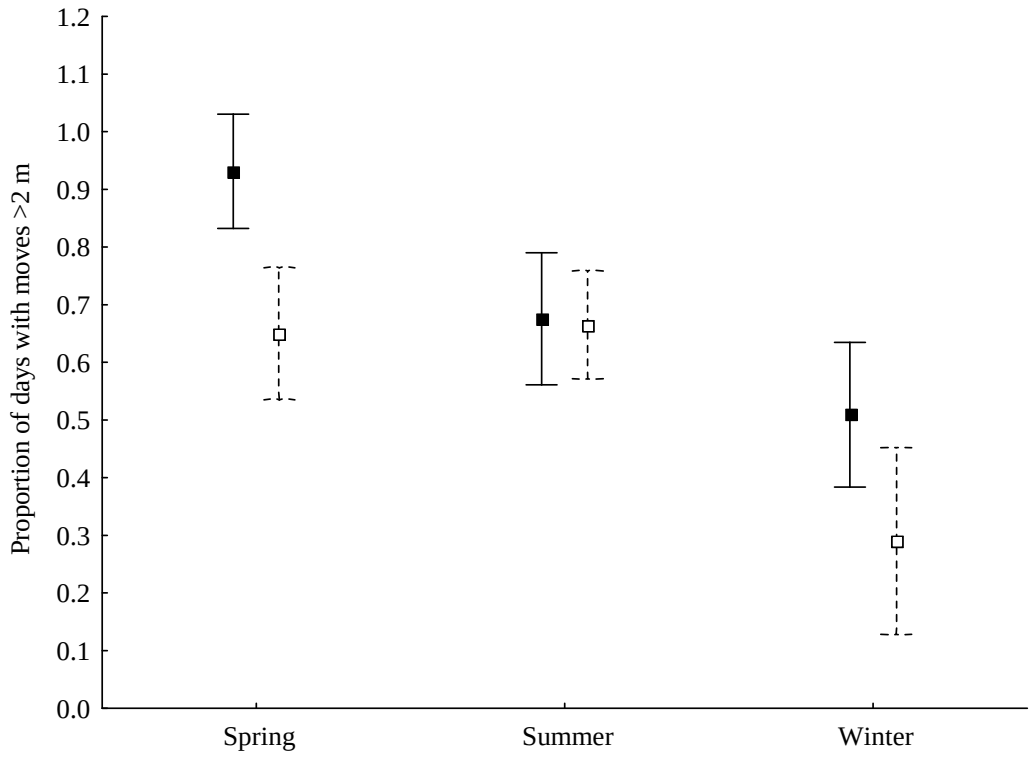


Figure 3.3: Proportion of days with movement greater than 2 m for male (solid) and female (dashed) *B. schneideri* during spring, summer, and winter months. Graphs show means and 95 % confidence limits.

3.3.4 To what degree are patterns of movement related to environmental conditions and prey availability?

In each season, the four measured environmental variables could be distilled down to two principal factors. In all cases, PC1 was dominated by the effects of air temperature and relative humidity, while PC2 was composed primarily of wind speed and atmospheric pressure (Table 3.1). The degree to which activity correlated with environmental variables differed across seasons. During winter, mean principal component vector for PC1 and PC2 were significantly different between observations of moving and non-moving snakes (Table 3.1). During spring, mean principal component vector for PC1 was significantly different between observations of moving and non-moving snakes (Table 3.1) but not significantly different for PC2. During summer, the mean principal component vectors for observations of moving and non-moving snakes were not significantly different, although differences in PC1 were nearly significant (Table 3.1).

Variation among Relative Activity Index for summer, autumn, and winter was negatively correlated prey availability ($r = -0.099$; $p = 0.033$) such that periods of little movement (and possibly frequent ambush behaviour) are associated with high levels of prey availability.

Table 3.1: The factor coordinates of each environmental variable to principal components one and two, for each radio telemetry season, as well as F test statistic for the comparison of each principal component between active and non-active snakes.

	Spring		Summer		Winter	
Variable	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
Air temperature	0.857	-0.369	0.893	0.321	-0.939	-0.108
Relative humidity	-0.901	0.071	-0.923	0.171	0.894	-0.024
Atmospheric pressure	-0.622	-0.067	0.260	-0.713	0.675	-0.261
Wind speed	0.373	0.909	-0.069	-0.816	0.099	0.975
F	8.240	0.899	3.654	0.280	13.283	5.047
p	**0.005***	0.344	0.056	0.596	**<0.001***	**0.026***

3.4 Discussion

Our analyses demonstrate that the activity patterns of Namaqua Dwarf Adders vary over the course of a 24 hour cycle, between seasons, and between sexes. Additionally our analyses demonstrate that bouts of activity are more strongly correlated with environmental conditions during winter, suggesting that it may be constrained during this season.

Our field observations, coupled with our observations of telemetered snakes show that Namaqua Dwarf Adders exhibit a peak in activity during the late afternoon. This pattern occurred across spring, summer and winter seasons, suggesting that the ecological pressures that drive it also do not vary seasonally. *Bitis schneideri* has traditionally been considered to be nocturnal (Branch, 1998), but this is based only on few, anecdotal observations and activity patterns of related species. Given that the most closely related species (*B. caudalis*) is generally nocturnal (Shine et al., 1998; DeNardo et al., 2002) and reduces activity levels in response to low ambient temperatures (DeNardo et al., 2002), it is possible that *B. schneideri* has become secondarily diurnal, shifting to diurnality in response to the cool coastal deserts of western southern Africa, where low night-time temperatures are not conducive to activity.

Compared to larger congenerics, Namaqua Dwarf Adders move relatively frequently. Male *B. schneideri* move on a nearly-daily basis during spring, and pooled data for females in spring,

and males and females in all other seasons suggest that snakes move on approximately two days out of every three (59.8 ± 18.3%). This contrasts strongly with activity levels of Gaboon Adders (*B. gabonica*) that move on approximately only 10% of days (Warner, 2009). Secor (1995) showed that Sidewinder Rattlesnakes (*Crotalus cerastes*), arid-adapted viperids from North America, move on approximately 32% of days annually, with a maximum of 60% of days during their active season. Conversely, active-foraging snakes are known to exhibit much higher frequencies of movement, with individuals of arid-adapted species such as *Masticophis flagellum* moving on approximately 75% of days (Secor, 1995). However not all ambushing viperids exhibit low movement frequencies. Marshall et al. (2006) demonstrated that Eastern Massasaugas (*Sistrurus catenatus*), small new-world viperids, moved relatively frequently (≈ 76% of days). Thus our estimates of movement frequency are within the recorded range for ambush foraging viperids.

The level of movement exhibited by Namaqua Dwarf Adders varied significantly across seasons. There was an obvious increase in the number of tracks observed during spring months, a pattern that was supported by telemetry data, showing that snakes moved more during spring than in other seasons. Moreover, male snakes were more likely to be active than female snakes during spring months. All of our observations (N = 4 pairs) of copulating Namaqua Dwarf Adders were made during the month of October, supporting the notion that increased male movement in spring is linked to mate-searching. The observed pattern of increased movement frequency in spring by males is mirrored by an increase in the mean distance moved during these periods (Maritz & Alexander, In Press-b).

Namaqua Dwarf Adders maintained a surprising level of activity during winter. In fact, snakes even continued feeding during winter months (Wessels & Maritz, 2009). While winter activity in snakes from sub-tropical latitudes is not uncommon, many other more temperate species in southern Africa are thought to fast through the winter months (Phelps, 2010). The general aseasonality of Namaqua Dwarf Adder biology may be due to the mediating effect of the Benguella Current off the west coast of South Africa.

Given the extent to which the behaviour of organisms is governed by environmental constraints, we expected variation in movement levels to be influenced by external factors to a greater extent than we recorded for *B. schneideri*. During spring months, movement was related to a change the principal component associated with air temperature and relative humidity. A similar, although not statistically significant, pattern was seen in summer.

However, during winter, movement was related to significant changes in both principal components, indicating that movement is restricted more directly by environmental conditions, even though activity levels are similar to levels in the other seasons.

Our data support the idea of activity being modulated by an array of ecological pressures. It is well known that high levels of activity make an organism vulnerable to predation (Gerritsen & Strickler, 1977). Additionally, reduced predation risk resulting from infrequent movement may be one of the potential pressures that have resulted in the evolution of ambush foraging. However, movement frequency can also be up-regulated through a need to find novel suitable ambush sites (Tsairi & Bouskila, 2004), alternative thermal conditions (Webb & Shine, 1998), and to avoid being detected by olfactory-oriented predators and prey (Burghardt, 1990; Downes & Shine, 1998; Kats & Dill, 1998). Our measures of movement frequency are high compared to some other ambushing viperids and we suspect that this is likely a result of a combination of these factors. Seasonally, activity levels can also be up-regulated by motivations such as the need to mate. The large increase in movement frequency exhibited by males, and concomitant observations of copulations during spring provides clear evidence of this motivation in our study system. Additionally, the relatively low movement frequency of females during spring supports the idea of predation risk modulated down-regulation of movement frequency. Finally, our analysis suggests that overall movement frequency is constrained by environmental conditions, but only obviously so during winter.

Our experimental design was limited by the range of times at which our observations took place since we were only able to track snakes during daylight hours. However, we do not believe that this logistic impediment greatly reduced the explanatory power of our data. We were able to integrate prevailing weather conditions with snake track counts, and with opportunistic observations, to be confident that Namaqua Dwarf Adders were not often active during the night. Moreover, the use of radio-telemetric techniques provided an unbiased assessment of activity patterns during the day because of the high detection probability associated with locating marked animals. Accordingly we are confident that our measures accurately describe activity in Namaqua Dwarf Adders.

Our study demonstrates that the timing of bouts of movement vary at different temporal scales. The observed pattern of movement over a daily-cycle was common to all seasons and similar to the pattern in environmental thermal conditions over this period, suggesting that movement at this fine temporal scale may be modulated by environmental conditions. At a

seasonal scale, however, environmental constraints appear to have a weaker effect on activity – only during winter (when we expect the availability of suitable thermal conditions to be constrained) did we find a strong relationship between environmental conditions and activity. Rather, variation in internal motivations to move, specifically mate-searching behaviour, appears to drive such broad-temporal scale variation in movement patterns.

The diurnal activity pattern shown by *B. schneideri* in our study provides evidence that the biology of arid-adapted organisms may be modified by the proximal, prevailing environmental conditions. Although *B. schneideri* occurs in a desert environment, prevailing temperatures in its range are greatly moderated and decreased due to the proximity to the Atlantic Ocean and Benguella Current. We postulate that the atypical diurnal activity pattern shown by *B. schneideri* is a derived condition and is a direct response to these conditions. Furthermore, we predict that similar responses may be expected in other species that occur in close proximity to this coastline.

3.5 Acknowledgements

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CHAPTER 4

DWARFS ON THE MOVE: SPATIAL ECOLOGY OF THE WORLD'S SMALLEST VIPER, *BITIS SCHNEIDERI*

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Abstract – Namaqua Dwarf Adders (*Bitis schneideri*) are small viperids that inhabit sandy coastal habitats within the Succulent Karoo Biome in southern Africa. Their ecology, and the faunal ecology within the region in general, is poorly documented, hampering effective conservation planning for this biodiversity hotspot. We used radio telemetry to investigate the spatial ecology of a population of *B. schneideri*. We measured mean daily displacement (MDD) of 19 male and 18 female snakes during the austral spring, summer, and winter. We also compared mean squared displacement from centre of activity range (MSD), a measure of home range area, for males and females between the three seasons. Finally, we compared MDD of another 60 individuals collected using mark–recapture techniques. In general, snakes did not move great distances. Males moved further during spring (47.3 ± 3.9 $m.day^{-1}$) than during summer (3.3 ± 4.5 $m.day^{-1}$) or winter (3.0 ± 5.0 $m.day^{-1}$). Female MDD did not vary significantly across spring (6.4 ± 4.6 $m.day^{-1}$), summer (2.7 ± 3.7 $m.day^{-1}$), or winter (0.8 ± 6.5 $m.day^{-1}$), nor was it different to the MDD of males during summer and winter. MDD in the mark-recapture group did not differ among adult males, adult females, or juveniles. Home range area estimates varied between sexes and within seasons, generally corresponding to patterns shown for MDD. Overall mean home range size was larger in males (0.85 ± 0.09 ha) than females (0.10 ± 0.09 ha). Our data suggest that gene flow in *Bitis schneideri* is likely to be facilitated through the movement of male snakes during spring. However, the relatively short distances over which males range (even the most mobile males are sedentary compared to other species), and the apparent lack of any significant dispersal in juveniles, implies that the species may be vulnerable to fragmentation at relatively fine spatial scales. Thus, conservation management of the Succulent Karoo, the biome to which the species is restricted, should be aimed at minimizing habitat fragmentation.

4.1 Introduction

The Succulent Karoo Biome of southern Africa represents one of few arid global biodiversity hotspots (Myers et al., 2000). The region exhibits remarkable levels of both diversity and endemism for the flora (Lombard et al., 1999) and fauna (Vernon, 1999; Myers et al., 2000; Le Roux, 2002). It is also very poorly protected (Driver et al., 2005), despite facing several threats including pressure from overgrazing (Lombard et al., 1999), mining (Driver et al., 2005), and climate change (Erasmus et al., 2002). However, the basic understanding of the biology of the organisms that inhabit this region, required to make informed conservation management decisions, is still severely lacking.

Namaqua Dwarf Adders (*Bitis schneideri*) are arid-adapted viperids that inhabit semi-vegetated coastal sand dunes along the southern African western coast (Broadley, 1983; Branch, 1998). Individuals of this species are recognised as the smallest viperids, reaching a maximum snout-vent length of no more than 255 mm (Branch, 1998; Maritz & Alexander, In Press-a). Our unpublished data also demonstrate that individuals occur at high population densities. *Bitis schneideri* is currently listed as Vulnerable by the IUCN (Branch, 1988; World Conservation Monitoring Centre, 1996). However, recent assessments, based on the discovery of additional localities and our ongoing ecological investigations indicate that the IUCN conservation status may change to that of Least Concern in the future. Nonetheless, information regarding the ecology of this species is of value to conservation managers because the fauna of the region (especially typical species such as *B. schneideri* which is endemic to part of the Succulent Karoo) remains poorly known. Additionally, ecological information from a wide range of species is needed to develop the holistic understanding of arid ecosystem processes required to conserve and manage such environments.

Movement patterns are an important component of the ecology of all animals (Nathan, 2008). In snakes, movement allows individuals to find feeding grounds (King & Duvall, 1990; Webb & Shine, 1997), thermally suitable retreats (Webb & Shine, 1998), overwintering sites (King and Duvall, 1990; Secor, 1994), and mates (Madsen et al., 1993). Moreover, measures of space-use can provide valuable insights into mating systems (Shine et al., 2001), risk of mortality (Bonnet et al., 1999), and conservation issues such as gene flow and habitat fragmentation (Clark et al., 2008). As a result, studies focusing on space-use by snakes, and snake ecology in general, have become increasingly popular in recent years (Shine and Bonnet, 2000). However, studies of the spatial ecology of snakes suffer from a strong

geographic (and thus phylogenetic) bias as the vast majority are concerned with species inhabiting the Americas, Europe, and Australia. Despite Africa's rich snake fauna (Greene, 1997), the spatial ecology of relatively few African snake species has been investigated. While there is an abundance of radio-telemetric studies on snakes in general, fewer than ten have focused on African snake species (Angelici et al., 2000a; Angelici et al., 2000b; Lawson, 2006; Linn et al., 2006; Alexander, 2007; Cottone, 2007; Warner, 2009).

In this paper we present the results of a study of the spatial ecology of a population of *B. schneideri*. Given the paucity of knowledge regarding the ecology of reptiles (especially snakes) from southern Africa, and the conservation issues associated with both *B. schneideri* and the Succulent Karoo Biome, our findings provide a valuable contribution to conservation managers working in this and other arid regions. Moreover, information regarding the ecology of the world's smallest viper can provide valuable insight into the evolution of this and other 'dwarf' species.

4.2 Materials and methods

4.2.1 Study site

We collected data on the movement patterns of Namaqua Dwarf Adders along coastal dune fields on the farm Noup, Northern Cape Province, South Africa (30°08′ S; 17°12′ E). Field observations (primarily by the senior author) took place on more than 420 days between September 2007 and July 2010. The study site was approximately 480 ha in extent and comprised primarily of young calcareous aeolian sands that form semi-vegetated longitudinal dunes (Desmet, 1996; Desmet & Cowling, 1999). The habitat was relatively homogenous, and was characterised by small succulent or sclerophyllous plants typical for Sandveld habitats along the coast (Mucina & Rutherford, 2006). The study site receives 50 - 150 mm rainfall per annum, and coastal fog is frequent (Cowling et al., 1999). More than 60 % of annual rainfall falls during winter (Desmet, 2007). Temperatures are moderated by the close proximity of the cold Benguela Current and are generally cool, ranging from a mean temperature of 14.3 °C in winter to 18.2 °C in summer (Desmet, 2007).

4.2.2 Radio-telemetry

We used radio-telemetry to investigate movement patterns of 18 female and 19 male adult individuals (Table 4.1). We actively searched for and captured snakes on the study site,

anesthetized them using vaporised isoflurane, and fitted each with a temperature sensitive radio-frequency transmitter (BD-2NT, Holohil Systems Limited, mass = 0.5 g). Transmitters were glued to the dorsal surface of the snakes using a cyanoacrylate adhesive, and were positioned slightly anterior to the tail, with the 140 mm whip antenna trailing behind the snake (Fig. 4.1). Although we did not quantify differences between telemetered and non-telemetered snakes, transmitters did not appear to influence movement, behaviour, or retreat site selection. We fitted transmitters to snakes heavier than 12 g to ensure that transmitter mass remained below 5 % of snake body mass. As a consequence of their small size, transmitters had short life-spans (21 days at 40 °C; according to manufacturer specifications). For this reason, and in order to quantify differences in seasonal movement patterns, telemetry work was performed on three groups of snakes during three austral seasons: spring (October 2009), summer (December 2008 - January 2009) and winter (July 2010; Table 4.1).

All telemetered snakes were released at their original point of capture within 7 days of initial capture. Each snake was located daily using a Communications Specialist R1000 handheld receiver and 3-element Yagi antenna. On the day that each transmitter was predicted to deplete its battery power, the relevant snake was recaptured, the transmitter removed, and the snake returned to its last known location. During each encounter we recorded the date and time, and bearing from last-known location (degrees) using a compass. We also recorded the straight-line distance to the previous location (m) using a 50 m tape measure for displacements of less than 100 m, and a handheld GPS device (Garmin *Etrex*; datum: WGS84) for displacements greater than 100 m.

We calculated mean daily displacement (MDD: $m.day^{-1}$) for each radio-telemetered individual (as a proxy for overall movement) as the sum of the lengths of all steps during the observation period, divided by the total number of days over which that individual was tracked. Using analysis of variance we tested for seasonal and sex effects in MDD. MDD data were log-transformed before analysis to meet the assumption of normality required for analysis of variance.



Figure 4.1: Coastal Sandveld habitat at our study site (A), and adult male *Bitis schneideri* fitted with an externally attached radio-transmitter (B), and an adult male *B. schneideri* fitted with a radio-transmitter in the process of ingesting a Namaqua Rain Frog (*Breviceps namaquensis*).

Table 4.1: Number of individuals, snout-vent length (SVL), mass, and duration of observation for 37 *Bitis schneideri*, fitted with radio transmitters.

	n		SVL (mm)		Mass (g)		Duration (days)	
Season	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Spring	6	8	219.33 ± 11.20	195.63 ± 10.16	23.13 ± 3.27	14.00 ± 2.37	12.00 ± 7.07	19.38 ± 2.26
Summer	9	6	215.44 ± 13.56	207.83 ± 7.73	21.87 ± 3.99	16.95 ± 1.85	25.33 ± 1.73	19.00 ± 5.69
Winter	3	5	220.67 ± 9.29	194.60 ± 24.05	20.93 ± 1.81	16.62 ± 7.01	19.00 ± 1.73	19.40 ± 0.89

4.2.3 Home range size

We calculated homerange size as the mean square of displacement from the geographic mean of all known locations (MSD; Slade & Swihart, 1983) for each telemetered individual. We used MSD as a measure of home range size as this method is known to require fewer data to provide a realistic estimation of home range area than traditional location-based methods (Giuggioli et al., 2006). We compared mean home range size among seasons and sexes using factorial analysis of variance. We also pooled all data and calculated the mean home range area for each sex.

4.2.4 Juvenile movement

As juveniles of this species are too small to carry transmitters (mean juvenile mass = 4.1 ± 0.9 g; Maritz & Alexander, In Press-a), we compared MDD of adult and juvenile snakes recaptured during a mark-recapture study. Search methods involved active searches for snakes across a 22 ha and a 16 ha plot on our study site. Survey effort totalled 629 observer hours over three consecutive austral summers (generally daily from September to March) beginning in September 2007. Each individual captured in the mark-recapture program was sexed by assessing relative tail length (Maritz & Alexander, In Press-a), marked by clipping ventral scales (Fitch, 1987), weighed, measured, and released at the point of capture which was recorded on a handheld GPS device (Garmin *Etrex*; datum: WGS84). For each recaptured individual, we recorded the straight-line displacement from the original point of capture using a GPS and the time interval between captures (number of days). Given the size of the study plots, our methods allowed us to detect displacements of between 0 m and approximately 900 m and 660 m for each plot respectively (equal to the longest axis of each plot). We calculated MDD as the total displacement (m) between captures over the duration between captures (days), and compared these measures between adult males, adult females, and juveniles using analysis of variance.

4.3 Results

4.3.1 Radio-telemetry

Mean daily displacement of telemetered snakes varied significantly across sexes and seasons (Factorial ANOVA: $F_{(2, 31)} = 6.27$, $p < 0.01$, Fig. 4.2). Tukey HSD post-hoc analysis revealed that during spring the MDD of male snakes (47.3 ± 3.9 $m.day^{-1}$) was significantly higher than

the MDD of females during spring (6.4 ± 4.6 m.day^{-1}), summer (2.7 ± 3.7 m.day^{-1}), and winter (0.8 ± 6.5 m.day^{-1}), and males during summer (3.3 ± 4.6 m.day^{-1}) and winter (3.0 ± 5.0 m.day^{-1}), which were all similar.

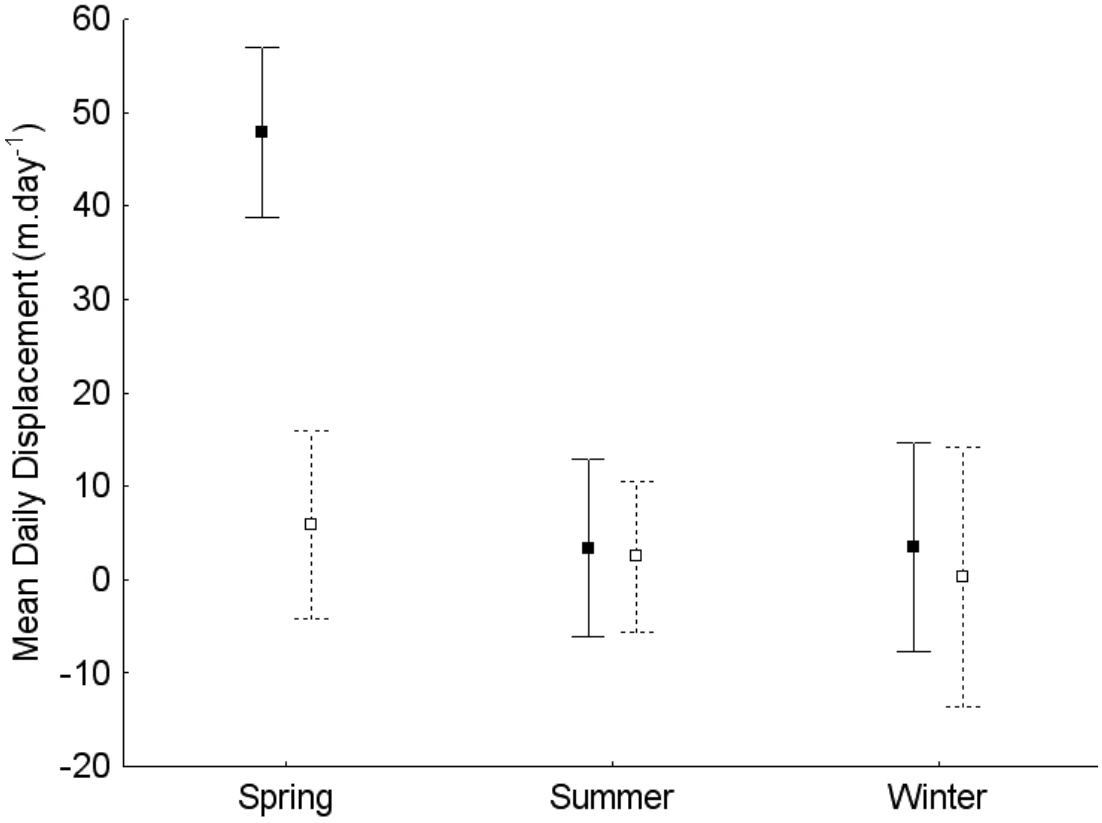


Figure 4.2: Mean daily displacement (MDD; m.day^{-1}) of female (dashed) and male (solid) telemetered *Bitis schneideri* during austral spring, summer and winter. Error bars represent 95% confidence intervals.

4.3.2 Home range estimation

Mean squared displacement from the center of activity range varied significantly among individuals (ANOVA: $F_{(36,\ 663)} = 31.03$, $p < 0.001$), but estimated home range was not significantly related to the number of observations of each individual (Spearman's Rank Order Correlation: R = 0.064). Estimates of home range area exhibited large variation and were not significantly different from one another (Factorial ANOVA: $F_{(2,\ 31)} = 3.18$, $p = 0.055$, Fig. 4.3), although Tukey Post-hoc analysis revealed that MSD of males during spring was significantly higher than all other measures of MSD. Males exhibited the largest home ranges (1.07 ± 0.21 ha) during spring. Home range estimates for males in summer (0.02 ± 0.25 ha) and winter (0.02 ± 0.27 ha) were similar to those of females during spring (0.02 ± 0.25 ha),

summer (0.02 ± 0.20 ha), and winter (0.001 ± 0.35 ha). Area estimates of home ranges of females snakes (mean ± SE = 0.10 ± 0.09 ha; max = 0.28 ha) were significantly smaller (ANOVA: $F_{(1, 698)} = 39.67$, $p < 0.001$) than the home ranges of male snakes (mean ± SE = 0.85 ± 0.09 ha; max = 1.03 ha).

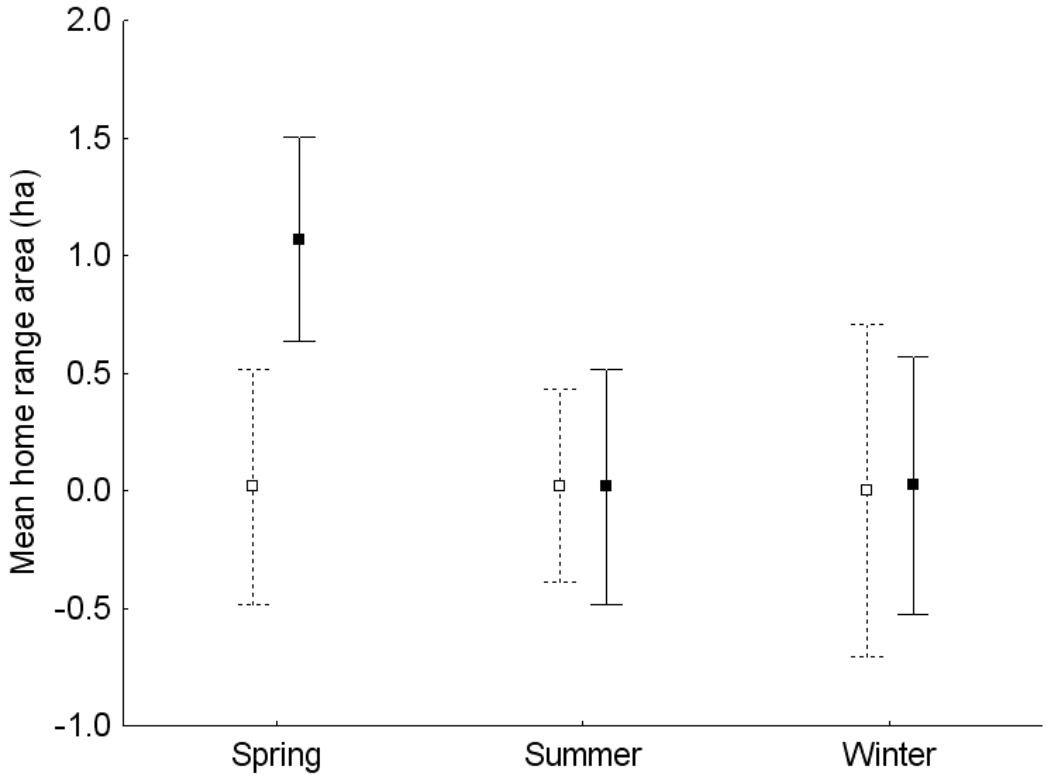


Figure 4.3: Mean home range area estimates for male (solid) and female (dashed) telemetered *Bitis schneideri* during austral spring, summer, and winter. Error bars represent 95% confidence intervals.

4.3.3 Juvenile movement

Active searches on our study site produced 340 individual *B. schneideri* (134 females, 145 males, 61 juveniles) of which 60 (23 females, 28 males, 9 juveniles) were recaptured at least once. ANOVA did not detect any significant differences in the MDD of adult females, adult males, and juveniles (ANOVA: $F_{(2, 56)} = 2.58$, $p = 0.08$, Fig. 4.4). MDD for males (3.8 ± 0.7 $m.day^{-1}$) and females (3.1 ± 0.8 $m.day^{-1}$) were similar and generally greater than the MDD for juveniles (1.1 ± 1.3 $m.day^{-1}$).

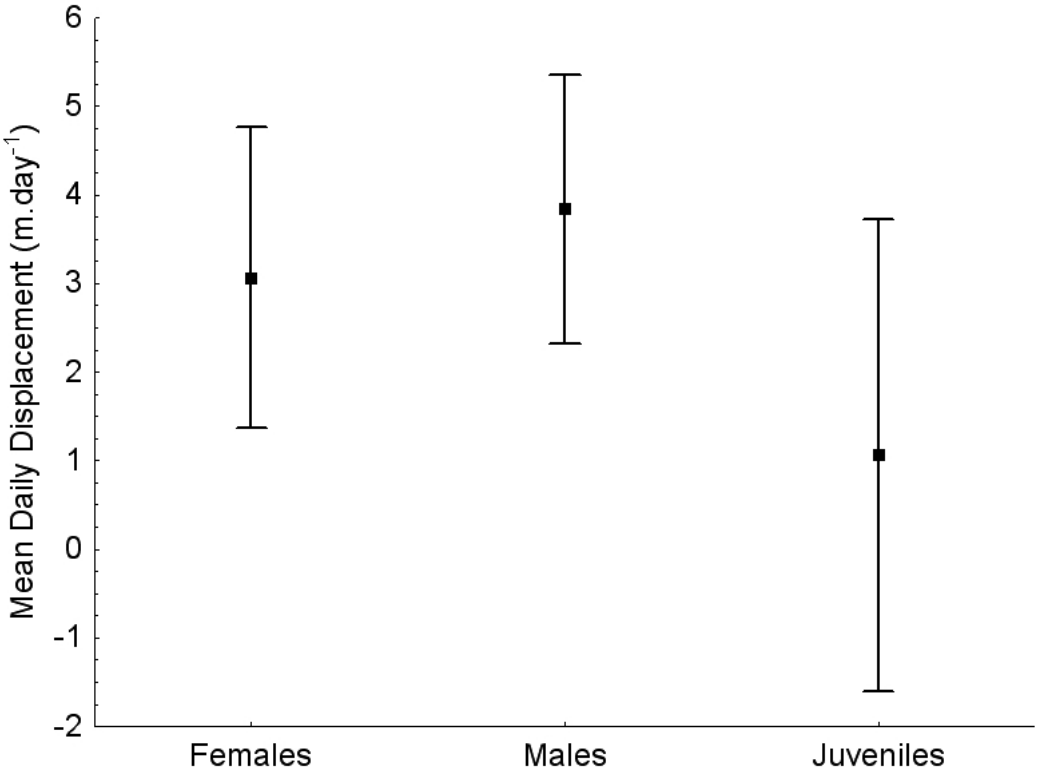


Figure 4.4: Mean daily displacement (m.day^{-1}) of recaptured adult female, adult male, and juvenile *Bitis schneideri*. Error bars represent 95% confidence intervals.

4.4 Discussion

In general, mean daily displacement of telemetered Namaqua Dwarf adders was low, ranging from 0.8 m.day^{-1} for females during winter to 47.3 m.day^{-1} for males during spring. Thus *B. schneideri* has a relatively sedentary lifestyle. Female snakes exemplified this lifestyle and showed low MDD in all seasons. The MDD of male Namaqua Dwarf Adders in summer and winter was similarly low suggesting that movement patterns of the two sexes do not differ during these seasons. It is likely thus, that the motivations for moving during these seasons do not differ between the sexes (e.g., movements that facilitate feeding or thermoregulation). However, MDD of male snakes during spring were significantly greater than both of the sexes in all other seasons. This increase is likely associated with mate searching activities during this period. Our field observations support this idea - during the austral spring, male and female snakes were found in close contact with each other, and this was the only time of the year during which we observed courtship behaviour.

Although the total number of individuals used to estimate mean home range area is small, our estimates are not correlated with sample size, suggesting that they are realistic. Seasonal home ranges for female snakes were similar in all seasons, suggesting an aseasonal pattern of space-use. This pattern contrasts strongly with the seasonal home range estimates for males, in which mean spring home ranges (1.07 ha) were on average more than 56 times greater than males during other seasons combined (0.02 ha).

Estimating the area of long–term home ranges of female snakes was easily achieved by calculating MSD of all females in all seasons. Our estimate of female home range area is particularly small (mean = 0.096 ha, range = 0 – 0.28 ha), even when considering the snake's small body size (MaCartney, 1988). The large seasonal variation in home range area estimates from males made our assessment of long-term home range more difficult. We define home range as the area utilised by an individual during the course of its activities. Such a definition would mean that the home range includes areas utilised during mate searching activities, even if these parts were used infrequently. Accordingly our estimate of home range area from the pooled seasonal data is likely to underestimate total male home range area. Instead it is likely that the spring time mate searching home range area represents a better estimate of long-term home range area in male *B. schneideri*.

Because our radio telemetry work was conducted on different groups of individuals during each season, it is difficult to be sure that snakes are not occasionally undergoing long migrations to new areas of activity, and thus utilising much larger home ranges. However, if this were the case we would expect snakes from the mark-recapture group to exhibit much greater displacements than our telemetered snakes. This was not the case, even though our survey plots were large enough to detect large movements. Additionally, there is no evidence to suggest that Namaqua Dwarf Adders make large seasonal habitat shifts typical of many other species (e.g., *Crotalus cerastes* – Secor, 1994; *Hoplocephalus bungaroides* – Webb & Shine, 1997) as snakes were found only in sand dune habitats during all seasons.

In general, the individuals of smaller-bodied species tend to occupy smaller home ranges than do individuals of larger-bodied species (Mace et al., 1984; but see MaCartney, 1988). Thus the small home ranges that we measured for *B. schneideri* are not surprising. However the small size of *B. schneideri* means that directly comparative home range area estimates are not readily available. Work on *Crotalus cerastes* (Secor, 1994) and *Sistrurus catenatus* (Marshall et al., 2006) showed that some small pitvipers have comparatively large home ranges. Several

other species of pitvipers are known to use small home ranges: the asian *Gloydius shedaoensis* has home ranges of < 0.3 ha (Shine et al., 2003), and the small and arid adapted *Crotalus pricei* has a home range of 0.2 - 2.3 ha (Prival et al., 2002). The elapid, *Hoplocephalus bungaroides* also exhibited relatively small home ranges, with adults occupying mean home range areas of 3.3 ha (Webb & Shine, 1997).

Comparison of MDD of recaptured snakes showed that, although not statistically significant, MDD of juveniles was lower than those of adult males or females. Although limited by sample-size, our analysis suggests that juvenile snakes are not highly vagile, and are unlikely to exhibit long-distance dispersal. The longest dispersal of an individual that was initially marked as a juvenile was 140 m, recaptured more than two years later. Such limited dispersal of juveniles is unlikely to be an artefact of study plot size given the size of our study plots.

We have demonstrated that Namaqua Dwarf Adders are relatively sedentary snakes that show low levels of dispersal. Accordingly, they may exhibit a limited capacity to overcome barriers to gene flow, and are therefore potentially vulnerable to habitat fragmentation. We would therefore expect limited gene flow between geographically proximate habitats, something that conservation managers need to consider when making decisions regarding the management of this habitat.

4.5 Acknowledgements

Ernst Oppenheimer and Son, the Rufford Small Grants Foundation, South African National Biodiversity Institute (SANBI) and the School of Animal, Plant & Environmental Sciences of the University of the Witwatersrand provided essential financial support to this project. Namaqualand Mines, D. McFadyen, and the Wessels family provided much needed logistic support. All protocols were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (2007/68/1 and 2007/69/3) and by Northern Cape Province Department of Tourism, Environment and Conservation (0914/07 and FAUNA 698/2009). Comments from S. Scott and S. Hanrahan helped improve this manuscript. A. Miller helped with the colour graphics.

CHAPTER 5

POPULATION DENSITY AND SURVIVAL ESTIMATES OF THE AFRICAN VIPERID, *BITIS SCHNEIDERI*

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Abstract – Estimates of population characteristics such as survival and density are essential for understanding and managing wildlife populations. Although such measures are available for several snake populations, most of these are for populations in northern temperate environments - few are available for African species. Here we present the results of a three-year mark-recapture study on the Namaqua Dwarf Adder (*Bitis schneideri*). We estimated survival, recapture probability, and population density by marking 279 snakes (121 males, 108 females, 50 juveniles) on two study sites along the Namaqualand coast. We recaptured 54 individuals (27 males, 23 females, 4 juveniles), yielding recapture rates of 20.4% and 17.9% at each site respectively. The adult sex ratio of our sample did not differ significantly from equality. We fitted eight models that included both individual-dependent and time-dependent covariates to our recapture data from each site, and compared models using Akaike information criterion corrected for small sample-sizes (AICc). Mean (± SD) estimated monthly apparent survival was low at both sites (0.86 ± 0.11 and 0.86 ± 0.12), as were mean recapture likelihoods (0.06 ± 0.04 and 0.06 ± 0.01). Population density estimates were similar for the two sites (7.52 ha^{-1} ± 3.62 and 8.31ha^{-1} ± 7.38). Juvenile snakes exhibited higher survival than adult females, which in turn, had higher survival than adult males. Additionally, juveniles had a lower recapture probability than adult males or adult females. We also estimated the likelihood of an individual leaving the study area during each month using 1000 simulated random-walks at each of two appropriately sized sites. Likelihood of emigration was 6.8% (± 0.5%) and 9.4 (± 1.0%) per month for the larger and smaller sites respectively. Based on our measures of apparent survival and emigration, we estimate annual survival rates of 35% and 45% for the two sites respectively. Our measures of population characters differ substantially from those of other viperids highlighting the need for additional studies of African snake populations.

5.1 Introduction

Robust estimates of population size calculated using mark-recapture techniques generally require large samples, and relatively high recapture rates. For species that are cryptic and exhibit low detection probability, such as many snakes, these data are difficult to collect. Additionally, working in difficult to access or politically unstable areas, makes fieldwork difficult and expensive to conduct. It is therefore not surprising that Africa, despite its remarkable snake diversity, remains enormously underrepresented in the field of snake population ecology (Parker & Plummer, 1987; Bonnet et al., 2002). Moreover, recent analyses describing global declines in snake populations (Reading et al., 2010) highlight the importance of population-based studies, especially in regions where biodiversity loss remains poorly quantified.

Most of the theory governing snake ecology has been derived from information garnered from a few well-studied, model species (see Seigel et al., 1987). Geographically, there is a strong bias to North America and Europe (Shine et al., 1998). While such studies have formed the basis for an increase in the use of snakes as ecological model organisms (Shine & Bonnet, 2000), there is little indication of whether they are representative of African species, especially given the phylogenetic distinctiveness of African snake lineages (Cadle, 1994). In fact, Janzen (1976) argues that snake abundance in Africa is generally lower than that found in the Americas and Australia, but this idea remains largely speculative.

Population characteristics such as abundance, density, and survival rate are essential in the development of an understanding of the autecology of an organism. While population estimates are available for several species of snakes globally (Parker & Plummer, 1987), relatively few of these have been robustly estimated using mark-recapture models (Koons et al., 2009). In Africa, the situation is confounded by the fact that the population ecology of very few species has been investigated. Madsen and Osterkamp (1982) analysed mark recapture data for a population of *Lycodomorphus bicolor* on Lake Tanganyika, while more recent work in West Africa has provided density estimates for a few, large, forest-associated species such as *Bitis gabonica*, *B. nasicornis* (Luiselli, 2006), and *Dendroaspis jamesonii* (Luiselli et al., 2000). Given the geographic extent and diversity of Africa, studies of four species, restricted to particular biomes, are unlikely to be representative of snake populations across Africa.

Here we present the estimates of population density, apparent survival, and recapture probability of an arid-adapted African viperid, the Namaqua Dwarf Adder, *Bitis schneideri*. This species is currently listed as Vulnerable by the IUCN (World Conservation Monitoring Centre, 1996) and is very poorly represented in museum collections (fewer than 50 specimens globally). It has traditionally been considered as rare (McLachlan, 1978) and our study was thus aimed at evaluating the conservation status of the species. Here, our primary objectives are to report on measures of capture probability (P), survival (φ), and density (D) for two populations that occur in the coastal dune system along the Namaqualand coast in South Africa.

5.2 Materials and Methods

5.2.1 Study species

Bitis schneideri is an arid-adapted viperid that inhabits coastal Sandveld habitats along the west coast of southern Africa (Broadley, 1983; Branch, 1998). It is the smallest viperid, with adults averaging 200 mm snout-vent length and not exceeding 254 mm snout-vent length (Maritz & Alexander, In Press-a). Our unpublished field observations strongly support the assertion that it is an ambush predator and that prey consists mainly of small vertebrates (Branch, 1998). The species is currently listed as Vulnerable by the IUCN as a result of habitat degradation over much of its distribution (Branch, 1988; World Conservation Monitoring Centre, 1996).

5.2.2 Methods

Our study was conducted on the farm Noup, in the Northern Cape Province, South Africa (30°08′ S; 17°12′ E). The study site has been described elsewhere (Maritz & Scott, 2010; Maritz & Alexander, In Press-a, b). We searched for Namaqua Dwarf Adders at two localities: a 27 ha ‘North Site’ and 16 ha ‘South Site’. The sites were similar with regards to topography and vegetation, differing only in area and distance from the coastline (South Site 0.8 km; North Site 2.6 km). Surveys were conducted over 17 months between September 2007 and March 2010. Search effort totalled 596 observer-hours, and was biased toward summer months when Dwarf Adders are more active and more likely to be encountered. Most snakes (88%) were located by following the distinctive tracks that moving individuals leave in the sand. All individuals that we encountered were captured by hand and marked by

clipping a unique sequence of ventral scales (Fitch, 1987). For each snake, we measured mass (to the nearest 0.1 g) using a digital balance, snout-vent length (SVL; to the nearest 1.0 mm) using a ruler, and sex (as either males, female or juvenile), based on obvious differences in tail length. Sex-based differences in tail length are not apparent in individuals smaller than 140 mm SVL and these were thus designated as juveniles (Maritz & Alexander, In Press-a). For each capture, we also recorded the date, time, and geographic coordinates of the location (using a handheld GPS device - Garmin *eTrex*, datum WGS1984). Additionally we recorded the total search effort (sum of the duration of all surveys) invested during each month.

In order to provide more accurate estimates of population parameters, we included two covariates in our analyses: SVL was included as an individual-dependent continuous variable that ranged from 99 mm to 251 mm, and allowed us to test for age effects on survivorship and capture probability. We also included survey effort as a time-dependent covariate, calculated as the total duration of all observations at a particular study site, during a particular capture occasion. We standardised this covariate so that it ranged between zero and one.

We fitted Cormack-Jolly-Seber models to recapture data from each site separately using the Mark-recapture Analysis package (McDonald, 2010) in R (R Development Core Team, 2009). We started by fitting a fully parameterised model (i.e., φ(svl) P(effort, svl)) to the capture histories from the two populations, and tested for goodness of fit using Hosmer-Lemeshow (Hosmer & Lemeshow, 2000), and Osius-Rojek (Osius & Rojek, 1992) goodness of fit statistics. We then fitted an additional seven reduced models (Table 5.1), and compared them using Akaike information criterion corrected for small sample sizes (Burnham & Anderson, 2002). To account for variation in model outputs we averaged all model estimates for φ, P, and N and weighted the contribution of each model using AICc weight scores.

To test for differences in the survival and recapture probabilities of adult males, adult females and juveniles, we averaged our estimates of φ and P for each individual, pooled the data for our populations, and tested for differences using single factor ANOVA. We used Tukey HSD Post-hoc tests to assess the statistical significance of paired contrasts.

Apparent mortality (1-φ) is comprised of those animals that do not survive to the next sampling occasion, as well as those that emigrate from the study site. The relative contribution of emigration to estimates of apparent mortality have been poorly investigated for most snakes (Parker & Plummer, 1987) but remains important in understanding overall survival. In order to estimate the likelihood of an individual having emigrated from our study

sites after 30 days (i.e., the likelihood that an animal initially detected on the study site will be absent during the following sampling occasion), we produced a random walk simulation model in Microsoft Excel, that placed 1000 individuals randomly within an appropriately-sized rectangular plot, and allowed them to move independently in a step-wise manner. Data collected from radio-telemetered individuals (see Maritz & Alexander, In Press-b) suggested no directional biases in movements, allowing us to model movements with random turning angles. Model movements were based on mean daily step lengths of 3.2 ± 4.8 $m.day^{-1}$ (Maritz & Alexander, In Press-b). Although this estimate of daily displacement under-represents the movement of male snakes during spring, our radio-telemetry work (Maritz & Alexander, In Press-b) suggests that male snakes return to a smaller central portion of their home-ranges after mate searching forays, and the increased spring movements of males are thus unlikely to have a significant impact on our estimate of emigration. We ran each cohort of 1000 individuals ten times, for each study site, and calculated mean (± standard deviation) likelihood of emigration of individuals at each site.

5.3 Results

Search effort totalled 346 and 250 observer-hours on the North and South Sites respectively. In total, we captured 279 snakes, comprising 121 males, 108 females, and 50 juveniles. Of these, 162 snakes (70 males, 67 females, and 25 juveniles) were captured at the North Site, and 117 individuals (51 males, 41 females, and 25 juveniles) were captured at the South Site. Twenty seven individuals (13 males, 11 females, and 3 juveniles) from the North Site were recaptured once, and six individuals (two males and four females) were recaptured twice. Nineteen individuals (ten males, eight females, and one juvenile) from the South Site were recaptured once, and two males were recaptured twice. Recapture rates from the North and South Sites did not differ from one another ($\chi^2 = 0.016$, $P = 0.68$) returning 20.4% and 17.9% of all marked animals respectively. The adult sex ratio for captured adult snakes was 1:1.12 (F:M), which was not significantly different from unity ($\chi^2 = 0.74$, $P = 0.39$).

We tested for overall goodness of fit of our most parameterised model at each site using the Osius-Rojek and Hosmer-Lemeshow goodness of fit tests. Goodness of fit tests provided no indication of a lack of fit at either the North Site (O-R: $Z = 1411.19$, $P = 0.99$; H-L: $H = 3.13$, $P = 0.37$) or South Site (O-R: $Z = 1032.81$, $P = 0.58$; H-L: $H = 4.75$, $P = 0.19$) which allowed us to continue to fit our suite of reduced models.

At both sites, the saturated model (φ(svl)P(svl, effort)) performed best (i.e., attained the lowest AICc score – Table 5.1). However, several other models scored similar AICc values: one model at the North Site, and four models at the South Site attained ΔAICc scores of less than two. We chose the saturated model from the candidate models at both sites on the basis of their relatively low AICc scores, and for the sake of congruence in models across our study sites.

Table 5.1: Relative performance of our eight candidate mark-recapture models. φ = Survival; svl = snout-vent length; P = monthly capture probability; effort = sampling effort.

Model	No. Parameters	No. Coefficients	North Site			South Site		
			AICc	Δ AICc	AICc weight	AICc	Δ AICc	AICc weight
φ(svl)P(svl, effort)	4	5	**314.30**	0.00	0.41	**197.85**	0.00	0.28
φ(svl)P(effort)	4	4	318.02	3.72	0.06	198.69	0.84	0.18
φ(svl)P(svl)	3	4	330.36	16.06	0.00	198.86	1.02	0.17
φ(svl)P(.)	3	3	333.80	19.50	0.00	199.80	1.95	0.10
φ(.)P(svl, effort)	4	4	314.32	0.02	0.41	201.56	3.71	0.04
φ(.)P(effort)	3	3	316.89	2.59	0.11	199.45	1.60	0.13
φ(.)P(svl)	3	3	330.37	16.07	0.00	202.63	4.79	0.03
φ(.)P(.)	2	2	332.70	18.40	0.00	200.55	2.70	0.07

At both sites, our saturated model suggested minor influences of SVL on either survival or recapture probability (Table 5.2). Search effort was positively associated with capture probability at both sites.

Table 5.2: Model outputs for the best models at our North and South Sites.

Site	Capture Variables	Beta	SE	Survival Variables	Beta	SE
North	Intercept	-6.30	1.24	Intercept	2.48	1.23
	Effort	2.51	0.60	SVL	-0.001	0.01
	SVL	0.01	0.01			
South	Intercept	-4.47	1.29	Intercept	5.52	1.90
	Effort	1.39	0.76	SVL	-0.02	0.01
	SVL	0.01	0.01			

Averaged estimates of φ and P were very similar for the two sites (Table 5.3). Because of differences in site area, the North Site produced larger estimates of N than the South Site. However, area-corrected density estimates for the two sites were similar (Table 5.3). Assuming that survival is fixed through the course of a year, our apparent monthly survival estimate of 0.86 translates into an annual apparent survival estimate of 0.19.

Table 5.3: Model-averaged estimates of φ, P, N, and density (D) for each study site. Density calculated as N divided by the area of the study site. φ = Survival; svl = snout-vent length; P = monthly capture probability; N = Number of individuals at site; D = population density (ha^{-1}).

	North Site				South Site			
	Φ	P	N	D	φ	P	N	D
Mean	0.86	0.06	203	7.52	0.86	0.06	133	8.31
SD	0.11	0.04	98	3.62	0.12	0.01	118	7.38
Range	0.57–0.91	0.01–0.24	99–388	3.7–14.4	0.33–0.96	0.03–0.11	22–357	1.4–22.3

Apparent monthly survival differed significantly among adult males, adult females and juveniles ($F_{(2,275)}$ = 116.34; P < 0.001), with juvenile snakes (0.93 ± 0.0063) exhibiting significantly higher (mean ± SE) survival, than adult females (0.84 ± 0.0049), who in turn

exhibited significantly higher survival than adult males (0.82 ± 0.0046). Recapture probability also varied significantly among adult males, adult females, and juveniles ($F_{(2,275)} = 295.11$; $P < 0.001$), however this significant effect was a result of juvenile snakes exhibiting significantly lower (0.036 ± 0.0011) recapture likelihood than adult males (0.066 ± 0.00082) and females (0.064 ± 0.00078).

The area of each site influenced likelihood of emigration from that site. At the larger North Site, mean (± SD) likelihood of emigration after 30 days was estimated to be 6.8% (± 0.5%), which was lower than the mean estimated likelihood of emigration for the South Site, 9.4% (± 1.0%). Using these estimates of emigration likelihood increases the estimated mean monthly survival to 0.92 and 0.95 for the North and South Sites respectively, which translate into annual survival estimates of 0.39 and 0.56 respectively.

5.4 Discussion

We have demonstrated that our *Bitis schneideri* study populations do not exhibit a biased sex ratio, experience very low apparent survival, and occur at relatively high population densities. Additionally we demonstrated that juvenile snakes exhibit relatively high apparent survival and relatively low recapture probabilities compared to adults. Adult males exhibit significantly lower apparent survival than adult females, but similar recapture probabilities. Finally, we demonstrated that emigration is likely to make up less than 10% of apparent mortality.

Our findings represent one of the first robust, empirical assessments of the survival rate, capture probability, and population density of any African snake. The general congruence among model outputs for the two populations support the authenticity of our findings. In general, our capture rates were low, and as a result many of the parameters that we have estimated are associated with wide confidence limits. However, such problems are unavoidable for cryptic organisms such as many snake species (Turner, 1977; Parker & Plummer, 1987).

Studies of African snake population dynamics are rare, making direct comparison of our result against African species difficult. To our knowledge, no other estimates of survival exist for an African snake population. Numerous studies on primarily European and North American populations suggest that (apparent) survival varies widely among snake species

(0.35 – 0.85; Shine & Charnov, 1992). More recently mark-recapture analyses of snake populations have reported survival estimates for viperids including *Vipera aspis* (0.75; Flatt et al., 1997), *Crotalus viridis oreganus* (0.55 – 0.82; Diller & Wallace, 2002), *Crotalus horridus* (0.82 – 0.95; Brown et al., 2007), and *Agkistrodon piscivorus* (0.79; Koons et al., 2009), colubrids including *Thamnophis radix* (0.35 – 0.45; Stanford & King, 2004) and *T. atratus* (0.56 – 0.64; Lind et al., 2005), and elapids including *Hoplocephalus bungaroides* (0.82; Webb et al., 2003) and *Rhinoplocephalus nigrescens* (0.74; Webb et al., 2003).

Our estimates of survival for *Bitis schneideri* (0.39 - 0.56) are low in comparison to the estimates reported above, especially in comparison to measures for other viperids. Shine and Charnov (1992) demonstrated a strong relationship between mean annual survival and age at maturity for snakes, with rapidly maturing species exhibiting lower annual survival rates. Maritz and Alexander (In Press-a) show that sexual maturity is reached at the age of ten to 15 months in *B. schneideri*. This rapid maturation and the low survival reported here fit the trend described by Shine and Charnov (1992).

Our finding that juvenile *B. schneideri* have higher survival rates than do adults may be the first corroborating evidence of Pike et al. (2008)'s prediction that juvenile snakes exhibit behavioural traits that reduce predation risk. In many ambush-foraging species (such as *B. schneideri* and other ambush-foraging snakes) bouts of movement are likely to pose increased predation risk (Bonnet et al., 1999). Given that mate-searching movements appear to be the motivation for the majority of movement in our study species (Maritz & Alexander, In Press-b, Maritz & Alexander, Submitted-a) and that juvenile snakes do not mate-search, then juvenile snakes may face greatly reduced predation risk and thus high survival. This idea is supported by our concurrent estimates of recapture probability that are relatively low (see below), and relatively low measures of daily displacement by juvenile snakes (Maritz and Alexander, In Press-b).

We calculated a mean recapture probability of ≈ 6% for our study population. Recapture probability was low compared with those estimated for other snake populations (Brown et al., 2007; Diller and Wallace, 2002; Lind et al., 2005). Our best models unsurprisingly demonstrated that recapture likelihood was strongly influenced by search effort, but showed that SVL had little influence on recapture probability. We detected no difference in recapture likelihood of adult males and adult females, despite males moving much further than female snakes during the spring mate-searching season (Maritz and Alexander, In Press-b). This

finding supports the hypothesis that outside of the brief mate-searching season, male and female snakes are exhibiting similar behavioural repertoires. Mean (± SE) juvenile recapture likelihood was low (3.6% ± 0.0011%), supporting our hypothesis of reduced movement during this life-phase.

Density estimates for African snake populations are also rare, making generalisations regarding African snake populations difficult. Luiselli (2006) estimated that both *Bitis gabonica* (0.16 ha^{-1}) and *B. nasicornis* (0.10 ha^{-1}) occurred at much lower densities than our measures for *B. schneideri*. Additionally, *Dendroaspis jamesonii*, a large elapid snake, is reported to occur at low population densities (0.11 ha^{-1}; Luiselli et al., 2000). Conversely, the aquatic *Lycodonomorphus bicolor* is reported to occur at densities of up to 380 ha^{-1} (Madsen & Ostercamp, 1982), but this measure may be inflated by snakes being attracted to a focal feeding point. Parker and Plummer (1987) reviewed snake population densities, and found that estimates of population density ranged from < 1 ha^{-1} (including the viperids *Crotalus cerastes, C. horridus,* and *C. viridis*) to more than 1000 ha^{-1} (*Diadophis punctatus* and *Regina alleni*). However not all of the estimates reported by Parker and Plummer (1987) are the result of robust mark-recapture analyses, and few are the result of models that simultaneously include estimates of recapture probability (e.g., Koons et al.,2009). Generally, viperid populations do not occur at densities greater than 10 ha^{-1} (Parker & Plummer, 1987). Two noteworthy exceptions are the island endemics *Gloydius shedaoensis* (≈ 273 ha^{-1}; Sun et al., 2001) and *Bothrops insularis* (≈ 55 ha^{-1}; Martins et al., 2008). While *B. schneideri* populations do not reach such extremes, our measures (7.52 ha^{-1} ± 3.62 and 8.31ha^{-1} ± 7.38) are still high compared to most viperid populations. Peters and Wassenberg (1983) demonstrated that for most groups of animals, smaller-bodied species tend to occur at higher densities. However, this pattern has not been unequivocally demonstrated for snakes (Luiselli et al., 2005). Nonetheless, *Bitis schneideri* is the smallest viperid making our relatively high density estimates unsurprising.

Partitioning the effects of mortality and emigration on apparent mortality is problematic, and remains one of the biggest challenges facing mark-recapture analysis. Most studies report apparent survival, as we have, but with little or no discussion of the contribution of emigration to those measures. Our random walk model showed that in the short term, emigration from the study site by a marked individual is relatively low (< 10%). *Bitis schneideri* individuals are relatively sedentary animals, occupying small homeranges (Maritz & Alexander, In Press-b). Given the generally size of our study sites, and the sedentary nature

of our study animals, the likelihood of a marked individual emigrating from the study site is more likely to be dependent upon the initial capture location of the animal – snakes captured closer to the boundary of the study plot have a greater likelihood of leaving the plot than those initially captured close to the centre of the plot. Accordingly, estimates of emigration likelihood are probably more sensitive to study plot size and shape, than to the duration of the study – increased duration gives snakes the time to emigrate, but is also likely to give them time to return to the plot. We therefore think that our estimates for a 30-day sampling occasion provide an appropriate estimate of emigration likelihood for our two sites.

If viewed as a proportion of apparent mortality, our simulations suggest that emigration could have important implications for the interpretation of survival estimates. Our measures of emigration show that it could make up 49% of apparent monthly mortality at the North Site and 67% at the South Site. Differences here are due to the difference in size of the sites. This finding also has important implications for other studies that have not factored emigration out of apparent survival measures. However, our emigration-corrected measures of monthly and annual survival are relatively low, and do not change our interpretations of our study system as one that experiences high mortality.

Parker and Plummer (1987) summarised the population traits of snakes, and described three major groupings. These were characterised by early-maturing temperate colubrids (low adult survivorship, low longevity, annual reproduction, high fecundity), late-maturing colubrids (high adult survivorship, high longevity, annual reproduction, low fecundity), and late-maturing viperids (high adult survivorship, high longevity, bi- or triennial reproduction, low fecundity). Of these groups, *Bitis schneideri* is more closely allied with early-maturing colubrids of temperate regions. Importantly, our data suggest that *B. schneideri* exhibits very different population characters to other viperids that have been investigated.

Our study represents one of very few studies that have empirically assessed population parameters for an African snake population. We have demonstrated that *Bitis schneideri* exhibits low recapture probability, experience high mortality rates, and occurs at relatively high population densities. Unfortunately, studies such as ours (focusing on African taxa) are scarce. The development of generalised theories that appropriately describe African snake ecology requires the study of additional African species. Until this situation is remedied, management actions related to African snake populations will remain speculative at best.

5.5 Acknowledgments

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CHAPTER 6

BITIS SCHNEIDERI MUST BREED ANNUALLY TO PERSIST: THE PROBLEM WITH BEING SMALL

Abstract – Reproductive frequency is an important aspect of reproductive output of an organism, and thus has important influences on organismal fitness. Viperid snakes, like many other ectothermic vertebrates, exhibit low reproductive frequency, whereby females only reproduce every second year, or even less frequently. However, for small-bodied species that have constrained clutch/litter sizes, and also experience low survival, low reproductive frequency may not produce sufficient offspring to sustain a population. I aimed to assess whether *Bitis schneideri*, a small, arid-adapted viperid snake from southern Africa exhibits low reproductive frequency typical of other viperids, despite producing small litters of offspring and experiencing low survival. I adapted the formula of Pike et al. (2008) to calculate the reproductive frequency required to sustain a population of *B. schneideri* that experience low survival, low mean litter size, and that become reproductively active at two years of age. I found that the small litter size imposed by being small-bodied, and low annual survival, require *B. schneideri* to reproduce frequently (probably annually) in order for populations to persist. I also dissected all available preserved female specimens to assess their reproductive status and found that five of the six females were reproductive, containing follicles, oviductal ova, or developing young. Such frequent reproduction is atypical among even closely related viperids, and appears to be facilitated through the capacity of *B. schneideri* to feed year-round in the aseasonal habitat in which they occur.

6.1 Introduction

Reproductive frequency (the number of clutches/litters produced by a female organism annually) is an important metric to the understanding the total lifetime reproductive output, and ultimately the fitness of an organism. It has a fundamental impact on the number of young entering a population over time and thus, ultimately, the viability of the population.

Despite its importance, it remains a poorly understood aspect of reproductive biology, especially among poorly studied groups of vertebrates such as snakes (Seigel & Ford, 1987).

Reproductive frequency in snakes ranges widely, from organisms that may produce multiple clutches annually (Tryon, 1984), to those that breed infrequently (Seigel & Ford, 1987), often in response to resource availability (Shine & Madsen, 1997; Madsen & Shine 2000). Low reproductive frequency (LRF; Bull & Shine, 1979) is a behavioural condition in which individuals of a species reproduce every alternate year, or even less frequently. The condition is widespread among ectothermic vertebrates (Bull & Shine, 1979), and is particularly common among viperid snakes (Seigel & Ford, 1987; Shine, 2003).

Measuring reproductive frequency is logistically difficult. Frequently, it is measured as the proportion of reproductive females among a sample of museum specimens (Seigel & Ford, 1987). Such data are difficult to collect when a species is poorly represented in collections and may also be misleading since the presence of follicles in the female reproductive tract does not guarantee that a female will reproduce that year (Seigel & Ford, 1987), or if females breed aseasonally or asynchronously. Despite these shortfalls, such data are valuable and form the basis of our understanding of reproductive frequency among snakes. Alternatively, reproductive frequency can be measured from the direct observation of wild populations (Vitt & Seigel, 1985), a method that is becoming easier with advances in technologies such as radio-telemetry. While field observations provide a more direct measure of reproductive frequency in a study population, such studies are time- and effort-intensive, making the collection of data difficult and expensive.

Reproductive frequency has an important effect in modulating population size. Pike et al. (2008) modelled survival rates of juvenile reptiles as a function of adult survival, mean clutch/litter size, age at first reproduction, and reproductive frequency. Using this approach it is possible to estimate the likely reproductive frequency for a stable population of equal sex ratio from information regarding survival, clutch/litter size, and age at first reproduction. Although this approach is contingent on knowledge of other aspects of the study organism's biology, it can provide a powerful tool for understanding the interaction of reproductive biology with other facets of biology such as survival, growth, and morphology.

Bitis schneideri is a small arid-adapted viperid that inhabits coastal dunes along the west coast of southern African (Broadley, 1983; Branch, 1998). In an effort to develop an improved understanding of the biology of the species, I investigated several aspects of its

ecology (Maritz & Scott, 2010; Maritz & Alexander, In Press-a, b; Maritz & Alexander, Submitted-a, b; Chapter 7). *Bitis schneideri* is poorly represented in museum collections (a total of fewer than 50 specimens in all major southern African collections) making adequate assessment of reproductive frequency through the dissection of preserved material challenging. However, Maritz & Alexander (In Press-a) provide information on age at first reproduction, while Maritz & Alexander (Submitted-b) report on survival rates in two wild populations of *B. schneideri*. When combined with measures of litter size, this information can provide estimates of reproductive frequency using Pike et al.'s (2008) approach.

Hedges (2008) demonstrated the importance of small body size in constraining litter size in snakes. *Bitis schneideri* is a small-bodied viperid (Maritz & Alexander, In Press-a) and females are thus likely to produce small litters. Moreover, *B. schneideri* has low survival rates (Maritz & Alexander, Submitted-b). I investigated reproductive frequency in *B. schneideri* using two approaches. Firstly, I dissected the few museum specimens available to us in order to measure the proportion of females in the sample that were gravid (or contained vitellogenic follicles). Next I derived measures of reproductive frequency based on our existing estimates of litter size, survival, and age to maturity. By doing so I aimed to assess whether LRFs typical of viperids would allow *B. schneideri* to persist given the constraints of body size and low annual survival.

6.2 Methods

Bitis schneideri is poorly represented in museum collections making the dissection of a meaningful number of preserved specimens impossible. However, during the course of our fieldwork, I encountered six female snakes that had been killed by motor-vehicles. I dissected all of these to examine whether they contained vitellogenic follicles or developing young. To support the evidence provided by museum specimens, I additionally investigated reproductive frequency using the approach of Pike et al. (2008). I rearranged formula 4 from Pike et al. (2008) to make annual reproductive frequency (n) a function of mean clutch size (c), juvenile survival (S_j), adult survival (S_A), and age at first reproduction (a) so that:

$$n = \frac{2(1 - S_A)}{(S_j)^a . c}$$

The parameters needed to solve for reproductive frequency were derived as follows:

6.2.1 Survival rates (adult and juvenile)

Maritz & Alexander (Submitted-b) derived annual survival estimates for adult *B. schneideri* from two populations (45% and 56%). I calculated the reproductive frequency required to sustain a population using survival rates ranging from 40% to 60%, encompassing the range of likely survival rates for adult snakes at our study site.

Maritz & Alexander (Submitted-b) demonstrated that juvenile survival was likely to be higher than adult survival. I thus varied annual juvenile survival between 44% to 66% in our model (set to be 1.1× adult survival).

6.2.2 Litter size

I chose a mean litter size of 3 offspring, but tested for sensitivity of our analysis by estimating reproductive frequency required to maintain a population for mean clutches of two, three, and four offspring per litter. These metrics were based on information from the literature (litter size of between two and seven; Haacke, 1975; Broadley, 1983; Branch, 1998) and from our own personal observations (litter size of 3; N = 3).

6.2.3 Age at first reproduction

Maritz & Alexander (In Press-a) showed that female *B. schneideri* grow rapidly and reach sexual maturity at approximately 15 months, suggesting that a female would be capable of breeding during the second spring of her life. Based on our observations of free-ranging snakes, I assumed mating to be seasonal, taking place in November, with females producing young during the following February.

6.3 Results

I was limited to very few adult female snakes for dissection. Of the six female snakes collected during field work, five (83%) contained follicles or developing young (Table 6.1). Although these data represent a very small sample, they do provide support for relatively high reproductive frequency in *B. schneideri*.

Table 6.1: Details of material examined in order to assess the proportion of reproductive female *B. schneideri*.

Field number	SVL	Date of collection	Status
BM161	210	10 October	Not reproductive
BM165	224	25 July	Oviductal eggs present
BM168	178	13 October	Two oviductal eggs present
BM193	208	10 December	3 mature follicles
BM194	207	10 December	3 mature follicles
BM196	222	12 December	3 mature follicles

Our calculations based on Pike et al.'s (2008) equation 4 produce measures of reproductive frequency between 0.45 and 3.04 litters.yr^{-1} for a stable population. The range in measures is the result of us varying the metrics of survival and litter size. Reproductive frequency was sensitive to changes in estimated survival rate and litter size (Fig. 6.1).

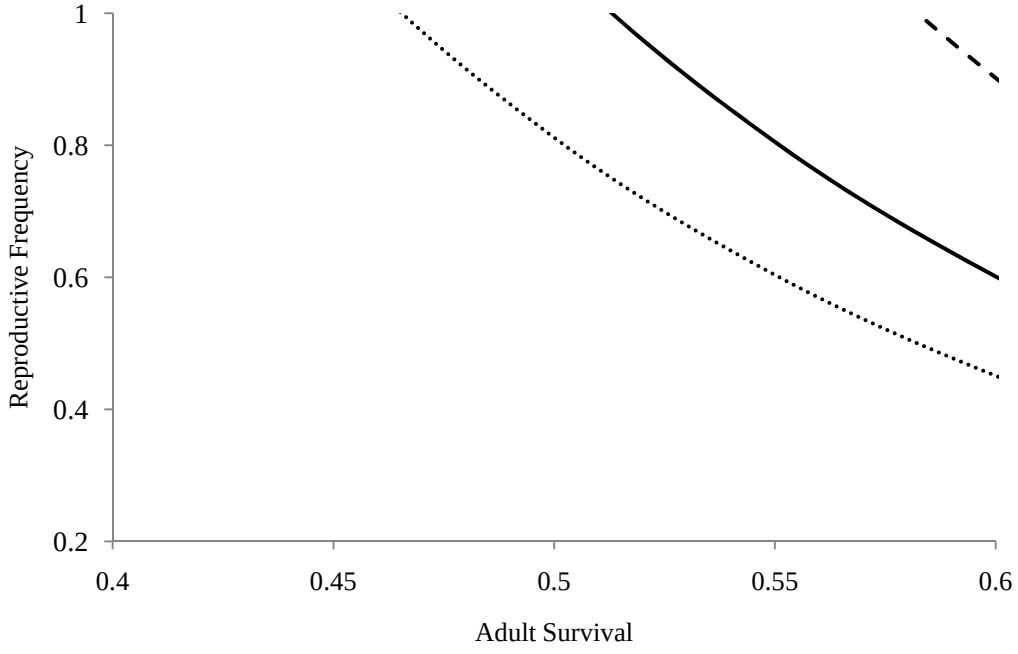


Figure 6.1: Reproductive frequency (*n*) as a function of annual adult survival rate (x-axis) and mean litter size to maintain a stable population (short dashes: mean litter size = 4; solid line: mean litter size = 3; long dashes: mean litter size = 2).

The calculated range of reproductive frequency effectively covered the range of likely reproductive frequencies, from annual reproduction, to biennial reproduction. However, for the most realistic measure of litter size (litter size = 3) and survival (≈ 50%; Maritz & Alexander, Submitted-b) reproductive frequency would need to be to be approximately annual (Fig. 6.1) to order to maintain a stable population.

6.4 Discussion

My results demonstrate that female *B. schneideri* reproduce frequently, as evidenced by the observation that a high proportion of the females that I dissected contained follicles or developing young. Moreover, small litter size and low estimated survival rates of *B. schneideri* mean that it is essential that females breed annually if the population is to persist.

A high proportion of female museum female specimens that I examined were reproductive at the time that they were preserved. By contrast, only 15% of female *B. caudalis* from arid habitats were considered reproductive by Shine et al. (1998). Even though not all females in our sample were reproductive, the link between body condition and reproduction in many snake species (Bonnet et al., 2002c) suggests a strong proximate role for energy surplus in reproduction. As a result, not all females would be expected to show signs of reproduction, even in an annually breeding species, and females that have recently given birth are unlikely show signs of their next litter. Thus, our finding of a high proportion of reproductive females provides support for the idea of *B. schneideri* reproducing annually.

Seigel & Ford (1987) reviewed the literature on reproductive frequency and found that most viperid species exhibited a low frequency of reproduction. Only three species listed in their review showed ≈100% of females as reproductive, and all three of those species (*Trimeresurus flavoviridis, Ovophis okinavensis*, and *Protobothrops tokanarensis*) are oviparous. Among viviparous viperids, most species exhibited LRF, with only four studies reporting proportions of reproductive females greater than 75%. Shine et al. (1998) have demonstrated that *B. caudalis* (the sister-species to *B. schneideri*) exhibits LRF, typical of viperids. These findings suggest that annual reproduction is uncommon among viperids and that it is likely a derived condition in *B. schneideri.*

Given that the most closely related species are all larger-bodied, reduction in body size of *B. schneideri* is likely to be a derived condition and can be viewed as a case of neoteny, whereby

adults exhibit smaller bodies typical of juvenile snakes. Maritz & Alexander (In Press-a) suggest that reduced body size in *B. schneideri* is a result of the selective advantages associated with the capacity to bury themselves into sandy substrates. Moreover, mean litter size is strongly correlated with maternal body size in most species (Shine, 1988; Hedges, 2008), and thus it is unsurprising that very small-bodied species (such as *B. schneideri*) have small litters. Because litter size is constrained in small-bodied species, the apparent relationship between litter size, annual survival, and reproductive frequency dictates that for species that have evolved small bodies, population persistence can only be maintained through an increase in reproductive frequency or survival (or both). Since *B. schneideri* has low survival, I thus expect females to reproduce frequently.

If mean litter size is constrained by body size in small-bodied species, population persistence becomes a trade-off between reproductive frequency and survival: a population can persist by breeding more frequently, or having improved survival. Few data are available to test this idea, primarily because of the limited number of studies that have quantified survival in snake populations (Parker & Plummer, 1987), especially small-bodied species. I predict that among small-bodied species, survival rate and reproductive frequency are likely to show a negative linear relationship typical of a trade-off between the two traits.

My calculations suggest that, in order to sustain a population at low levels of annual survival, a species with low mean litter size should produce more than one litter annually. Although Tryon (1984) reported that several species (oviparous and viviparous) are capable of producing multiple broods in a year, Seigel & Ford (1987) state that no conclusive evidence exists for this taking place in the wild, citing the high levels of food provided in captivity as an explanation for the behaviour in captive animals (but see Brown & Shine, 2002). These ideas support the assertion that food availability has the potential to be a proximate limiter of reproductive output in snakes (Shine & Madsen, 1997; Madsen & Shine, 1999a; Madsen & Shine, 2000). Importantly, it also means that for *B. schneideri* to breed annually, as required by the combination of small litter size and low survival, snakes need to be able to overcome the limited energy intake associated with ambush predation (Secor & Nagy, 1994). Energy intake in *B. schneideri* is not well understood but individuals may be able to overcome limited rates of energy intake by feeding throughout the year (Wessels & Maritz, 2009). Year-round feeding is probably facilitated by the relatively aseasonal environment produced by the moderating effect of the Atlantic Ocean.

One consequence of the neotenic adaptation of reduced body size in *B. schneideri* is a requirement for increase in reproductive frequency (to reproduction annually) in order to compensate for reduced litter size, and relatively low annual survival. *Bitis schneideri* may well be unique in this regard in that litter size is constrained by small body size, and that characteristics of their habitat sandy substrates and that year-round food availability (despite the temperate climate), allow them to achieve increased reproductive frequency.

CHAPTER 7

THE ENERGETIC ADVANTAGES OF CONSUMING VERY LARGE PREY: FORAGING ECOLOGY OF THE AFRICAN AMBUSH PREDATOR, *BITIS SCHNEIDERI*

Abstract – Ambush predators, and particularly snakes that ambush prey, are known to consume relatively large meals. While the costs associated with consuming large meals have been investigated, few studies have attempted to quantify the relative advantages of consuming very large meals, primarily because the frequency with which such prey items are encountered by wild snakes remains unknown. I quantified prey availability and feeding preferences for the African viperid *Bitis schneideri* in order to understand the advantages of consuming very large meals. I used captures from 4185 pitfall trap-nights to quantify the prey community available to ambushing snakes. Additionally, I used observations of feeding by wild snakes, and examined the stomach contents of road-killed snakes to quantify the relative abundance of prey types in the diet of *B. schneideri*. Finally I used an individual-based modelling approach to estimate the relative energetic advantages of the capacity to consume very large meals (largest 5% of prey items in the prey community). I found that the prey community at my study site was dominated by lizards, particularly *Meroles knoxi*, and that community structure did not vary significantly between seasons. Moreover I found a strong, positive correlation between the relative abundance of prey types in my traps, and in the diet of *B. schneideri*, suggesting that they are generalist feeders that consume prey types proportionally to the rate at which those prey types are encountered. I found that the distribution of availability of prey, and thus energy, was right-skewed, and that very large meals were encountered infrequently by ambushing snakes. However, my modelling suggests that even when snakes only rarely encountered large meals, the ability to consume them increased energy intake by 1.3 times. I propose that this represents a strong selective force, especially given the strong relationship between energy intake and reproductive output in snakes.

7.1 Introduction

Predators are known to exhibit a continuum of foraging modes, ranging from ambush predation, to active foraging (Pianka, 1966; Schoener, 1971; Gerritsen & Strickler, 1977; Pianka, 1978; Perry, 1999). Particular ecologies, physiologies, and morphologies correlate with foraging mode, and this is most obvious when foraging mode is near either extreme of the continuum (Secor & Nagy, 1994; Secor 1994; Secor & Diamond, 1998; Greene, 1997; Secor & Ott, 2007). A correlate of ambush-foraging behaviour is the capacity to consume large meals (Greene, 1997; Secor & Diamond, 1998; Secor & Ott, 2007). Being gape-limited predators, snakes have generally developed the capacity to consume relatively large prey items, and some snakes are able to consume meals that exceed their own body mass (Greene, 1997; Secor & Diamond, 1998). This is particularly true of the pythons, boas, and vipers. Morphologically, the capacity to consume such large meals has been related to a stout body form, relatively large head and highly fragmented scalation on the head (Shine, 1980; Greene, 1983), typified among viperids by members of genera such as the American *Crotalus* and African *Bitis*. Ambush-foraging Australian elapids (i.e., *Acanthophis* spp.) show morphological convergence with viperids, most likely as a result of foraging mode (Shine, 1980).

Ambush foraging is often associated with low prey encounter frequencies (Gerritsen & Strickler, 1977). The need to take advantage of infrequent prey encounters may have thus been the selective pressure that has resulted in the ability of ambush predators to capture and consume large prey. Consuming large meals is known to be associated with particular costs, specifically increased handling time (Cruz-Neto et al., 2001) and digestion costs (Secor & Diamond, 1995). While several studies have aimed to quantify the costs of consuming, few have investigated the energetic advantages of consuming very large meals, primarily because the frequency with which such large meals are available to wild snakes is unknown.

I investigated the foraging ecology of a population of *Bitis schneideri*, an arid-adapted viperid from the west coast of southern Africa. My study system presents a unique opportunity to answer questions related to prey availability for two reasons: *B. schneideri* is the smallest viperid (Maritz & Alexander, In Press-a), and since snakes are gape-limited predators, small snakes are likely to include a smaller range of prey sizes, and thus prey types, in their diet (Arnold, 1993). Also, Namaqua Dwarf Adders inhabit a structurally simple habitat, and are

entirely terrestrial, making it possible to measure the range of prey items available to the snakes.

My objective was to measure the primary metrics of the feeding ecology of Namaqua Dwarf Adders. This included quantification of the relative abundance of the various prey species, meal sizes and energy content, and prey encounter rates with snakes. I also show that Namaqua Dwarf Adders are generalist feeders, and consume prey in proportion to their availability, and accordingly I was also able to investigate the energetic advantage of the ability to consume very large meals using computer-based simulations. I demonstrate that large meals represent energy jackpot bonanzas, which provide snakes with substantial benefits. This may explain the evolution of the typical stocky body/large head morphology typical of ambushing snakes.

7.2 Methods

7.2.1 Study site

The study was conducted on the farm Noup, in the Northern Cape Province, South Africa (30°08′ S; 17°12′ E). The study site has been described in detail elsewhere (Maritz & Alexander, In press-a, b; Maritz & Alexander, Submitted-a; Maritz & Scott, 2010). Climatic conditions are moderated by the cold Benguella current, and as a result seasonality is limited – mean summer and mean winter temperatures differ by less than 4 °C, and although more frequent in winter, precipitation (predominantly convection fog, but also rainfall) occurs in all seasons (Robinson & Seely, 1980; Desmet, 2007). My investigations were conducted in stable dune habitat within the study site, where *B. schneideri* is most abundant.

7.2.2 Prey trapping

I used six pitfall trap-arrays to measure prey availability to ambushing snakes. Each array consisted of nine 10-litre plastic buckets (230 mm diameter; 240 mm deep), buried flush into the sandy substrate. Pitfall traps were installed in three rows of three pitfall traps, each separated from the nearest bucket by approximately ten meters and drift fences were not used. Traps were kept open for periods of between ten and 15 days, depending on logistical constraints. After a trapping session was completed, all buckets were left *in situ* and filled with sand so that a new session could be initiated simply by emptying the buckets. Trapping sessions were separated by at least 14 days and during trapping, buckets were inspected daily.

Captured animals were removed and released within 1 m of the pitfall trap. Animals of the same species and similar size, captured in the same trap on consecutive days were considered to be recaptures (this occurred on very few occasions). In order to estimate the body mass distribution for each prey type, I weighed a sub-sample of the captured prey items to the nearest 0.1 g, using a digital field balance. Trap effort was not equal in all seasons, totalling 986 trap-days, 1710 trap-days, 834 trap-days, and 655 trap-days in spring, summer, autumn and winter respectively.

Since some prey species exhibited bimodal mass distributions due to the presence of more than one demographic cohort, I separated these into two categories. I calculated the relative abundance of a prey type as the abundance of that particular prey type, divided by the sum of all other captures at a particular trap-array session, and averaged these measures across each trap array session. I used Kruskal-Wallis ANOVA to compared mean relative abundance between prey types, and Analysis of Similarity (Clarke & Gorley, 2001) to compare prey communities in each season.

Since other aspects of my field investigation involved measuring growth and survival of *B. schneideri*, I refrained from palpating individuals to induce regurgitation. As a result, the information on the diet of *B. schneideri* from the study population was limited to direct observations of wild snakes feeding, of gut contents of specimens killed by vehicles, and a single case of a regurgitated prey item. I compared the relative abundance of prey types in the diet of snakes, with the relative abundance of prey types trapped on the study site using correlation analysis.

7.2.3 Simulation of prey encounter rate

I estimated the energy content of prey items by using published energy conversions. I assumed wet mass energy contents of 8 $kJ.g^{-1}$for mammal tissue (Secor & Diamond, 1995). Estimated energy content of lizard tissue was based on the equation of Vitt (1978), and the energy content of amphibians was based on water content and energy estimates of Dierenfeld et al. (2002). I simulated a standardized energy availability frequency distribution by producing a prey community of 10000 virtual individuals comprising prey types at representative relative abundances, whose mass was drawn randomly from a normal distribution with the mean and standard deviation of the weighed sample of that prey type.

Finally, using an individual-based modelling approach, I simulated energy intake of an ambushing snake. Encounters occurred with a probability based on the mean daily encounter probability of each prey type in each season (i.e., the number of captures of that prey type during each trap-array session, divided by the total number of trap-days that the array was open, averaged across each trapping array session). I assumed that 13% of encounters with prey items were successful (see Clarke, 2006, for measures on percentage successful strikes). I calculated the annual energy intake of an ambushing snake as the sum of the energy content of all successfully captured prey items in a year. Our estimates of mean (± SD) annual energy intake are based on simulations of 1000 model runs each. I compared mean energy intake of snakes capable of consuming very large meals (largest 5% of prey population) with mean energy intake of those incapable of consuming very large meals using a paired t-test.

The estimates of mean annual energy intake are likely to be sensitive to the efficacy of the traps, and the measures represent minimum prey encounter likelihoods (the buckets were probably more obvious to prey than were ambushing snakes). I therefore investigated the sensitivity of the model outputs to various encounter probabilities, corresponding to 1×, 2×, 3×, 5×, 8×, and 10× trap efficacy. While the sensitivity analysis was primarily aimed at assessing the sensitivity of my findings, it had the added advantage of outlining the effect of increasing overall prey abundance on food intake rates.

7.3 Results

I captured 240 prey items representing nine species (six lizard, two mammals, and one amphibian species) over 4185 trap-nights resulting in an overall daily encounter rate of 0.057 encounters.trap^{-1}.d^{-1}. Where prey body mass distributions were bimodal for a species, I treated each size class (large vs. small) of each species as a separate prey type. Mean mass and accordingly energy content varied approximately 60-fold among prey types (Table 7.1).

Prey communities did not vary among seasons (ANOSIM: Global R = -0.005, P = 0.52) allowing us to pool the data. Overall prey type abundance varied significantly between prey types (Kruskal-Wallis: $H_{(12,507)}$ = 81.44, P < 0.001; Fig. 7.1). *Meroles knoxii* was the most abundant prey species captured by traps, making up approximately 40% of all captures.

Table 7.1: Mean (± standard deviation) mass and energy content of prey types accessible to *Bitis schneideri*. Energy content based on assumed energy content values of (see text for details). n = sample size of weighed animals, N = Total number of captures of each prey type. * Mass data for *Crocidura flavesence* from Skinner & Chimimba (2005).

Species	Size category	Mass (g)	Energy (kJ)	n	N
Breviceps namaquensis	Large	14.81 ± 3.79	77.09 ± 29.95	6	17
Breviceps namaquensis	Small	5.10 ± 1.96	23.04 ± 8.88	10	26
Crocidura flavesence	Large	30.00 ± 5.10	240.00 ± 40.8	*	3
Mus spp.	Small	3.07 ± 0.41	24.52 ± 3.27	9	20
Meroles ctenodactylus	Large	13.12 ± 0.40	114.11 ± 33.3	2	5
Meroles ctenodactylus	Small	2.14 ± 0.23	23.31 ± 1.93	2	2
Meroles knoxii	Large	4.06 ± 1.35	39.22 ± 11.2	11	49
Meroles knoxii	Small	1.28 ± 0.43	16.20 ± 3.58	22	47
Pachydactylus austeni	All	1.35 ± 0.30	16.85 ± 2.47	12	28
Trachylepis capensis	All	13.06 ± 5.72	113.62 ± 47.31	3	4
Trachylepis cf. homalocephala	All	12.6 ± 5.29	109.85 ± 42.32	3	5
Trachylepis varia	Large	2.71 ± 0.37	28.03 ± 3.02	4	22
Trachylepis varia	Small	0.45 ± 0.35	9.38 ± 2.92	3	12

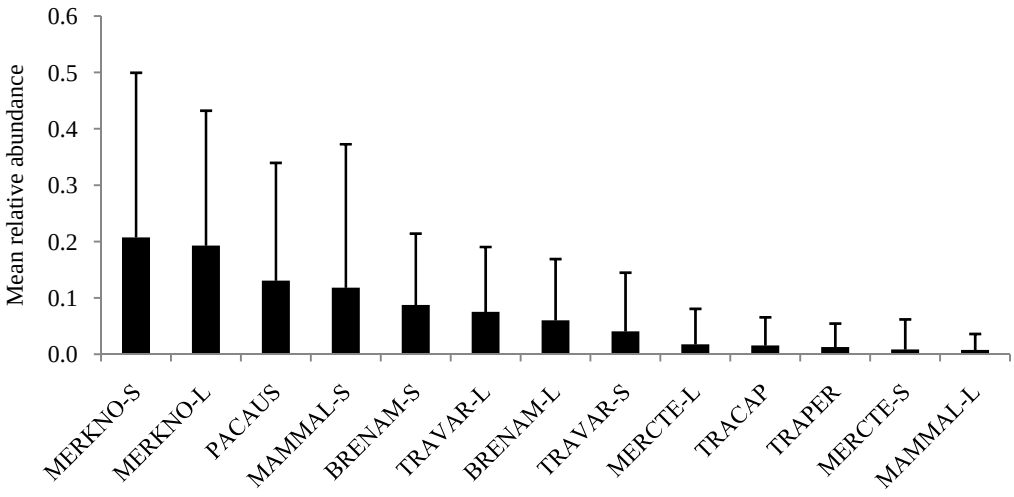


Figure 7.1: Mean (± SD) relative abundance (i.e., the number of captures of that prey type, divided by the sum of all other captures) of prey types per trapping session captured from 4185 trap-nights of pitfall trapping.

I recorded 13 instances of feeding over the course of the study (Table 7.2). Feeding was observed in all seasons except autumn. My observations highlight two important aspects of *B. schneideri* feeding ecology: Firstly, *B. schneideri*, like most ambush-foraging snakes are capable of killing and consuming relatively large meals. I collected a juvenile snake (SVL + tail length = 105 + 10 mm, mass = 4.3 g, Fig. 7.2) that had consumed an adult *Meroles knoxii* (SVL + tail length = 55 + 63 mm, mass = 4.3 g). Secondly, I noted that large snakes do not exclude small prey items from their diets, as evidenced by the observation of an adult male snake (SVL + tail length = 219 + 25 mm, mass = 19.1 g) consuming a *Trachylepis variegata* (SVL + tail length = 27 + 28 mm, mass = 2.1 g) representing a relative prey mass of only 11%.



Figure 7.2: Juvenile *Bitis schneideri*, with regurgitated adult *Meroles knoxi*.

Table 7.2: Feeding records collected during 17 months of fieldwork between September 2007 and March 2010. I observed no feeding during limited fieldwork during autumn.

Prey species	Season	Frequency of occurrence
Meroles knoxii	Spring	x 5
Breviceps namaquensis	Spring	x 3
Trachylepis variegata	Summer & Winter	x 3
Pachydactylus austeni	Summer	x 1
Bradypodion occidentale	Winter	x 1

The frequency with which I recorded prey types in the diet of snakes was strongly positively correlated (Pearson r = 0.90, p = 0.001, Fig 7.2) with the relative abundance of those prey types collected in pitfall traps. This finding provides strong empirical support for *B. schneideri* being a generalist predator.

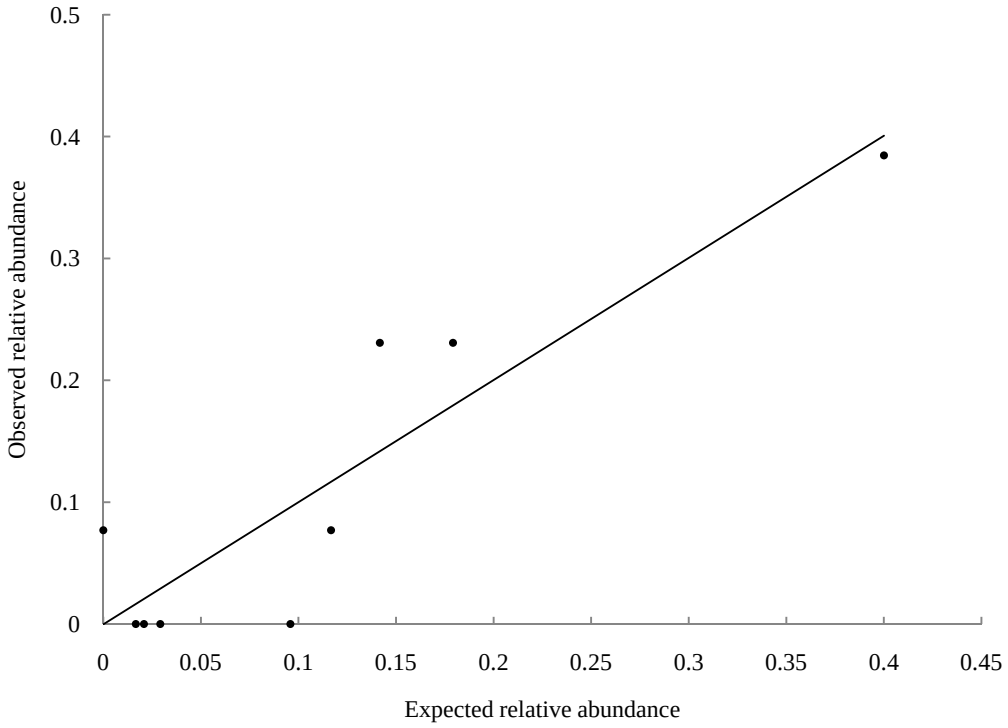


Figure 7.3: The relationship between expected relative abundance of prey species (based on relative abundance in pitfall traps) and observed relative abundance of prey species (based on feeding observations and gut content of road-killed animals).

I simulated the standardised frequency distribution of prey energy content by creating ten replicates of a community of 10000 prey animals, comprising thirteen prey types that varied in their relative abundance (as shown in Fig. 7.1) and varied in their mean energy content (Table 7.1). The resultant frequency distribution is strongly right-skewed (Fig. 7.4; gamma distribution).

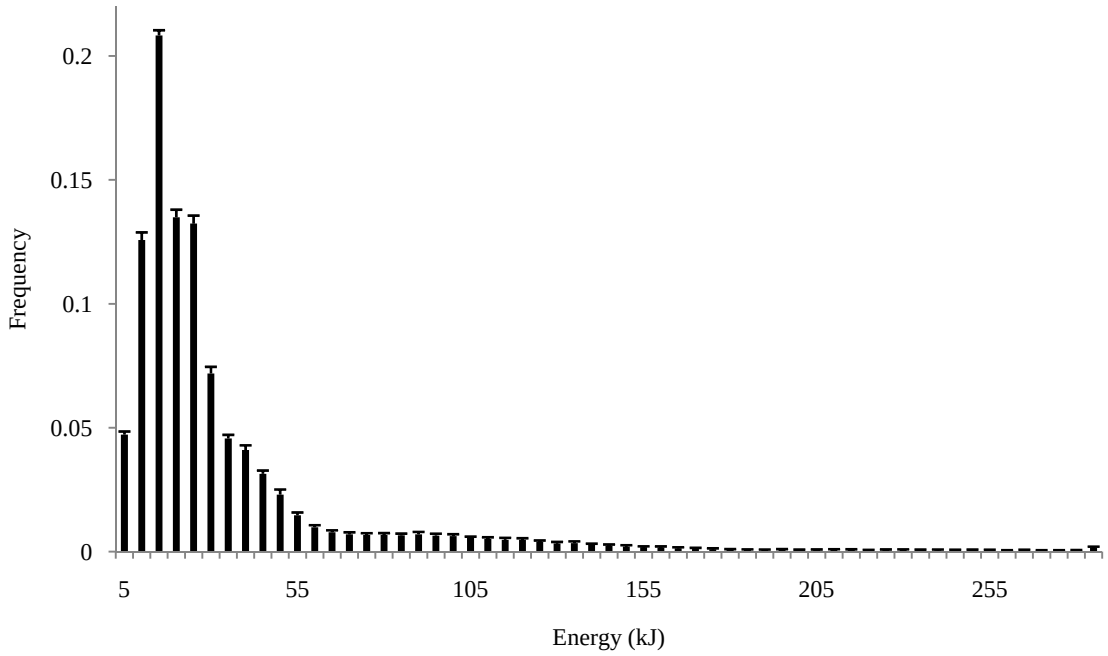


Figure 7.4: Mean (± SD) standardised frequency distribution of prey energy content available to an ambushing snake. Since *B. schneideri* are likely to consume different prey types proportionally to their relative abundance (see Fig. 7.1), the above frequency distribution also represents the relative likelihood of snake procuring a meal of any particular energy value.

Mean energy intake of snakes that could consume very large meals was significantly higher ($T_{(5)} = 3.42$, $p = 0.019$) than mean energy intake of those that could not, at all levels of prey encounters (Table 7.3). Mean energy intake increased linearly with increasing prey availability, but the factorial increase in energy intake associated with the capacity to consume large meals was approximately 1.3 at all levels of prey availability.

Table 7.3: Simulated mean energy intake for snakes that include, or exclude, very large meals in their diet, at various levels of prey encounter rates.

Prey encounter correction factor	Mean (± SD) energy intake excl. very large meals	Mean (± SD) energy intake incl. very large meals	Factorial increase in energy intake associated with consuming very large meals
1	84.8 ± 58.49	112.46 ± 87.35	1.3
2	160.10 ± 80.30	202.70 ± 112.33	1.3
3	242.61 ± 100.73	313.29 ± 143.36	1.3
5	401.24 ± 130.59	504.69 ± 181.54	1.3
8	633.74 ± 155.36	818.57 ± 245.33	1.3
10	798.63 ± 172.77	1014.54 ± 262.55	1.3

7.4 Discussion

My data show that *Bitis schneideri* is a generalist predator that consumes a variety of prey types approximately proportionally to the frequency that those prey types are encountered. Moreover, the relative abundance of prey types available to ambushing snakes, and the mean estimated energy content of those prey types, suggest an available-energy encounter frequency distribution that is right-skewed, with a long right tail. This has important implications for foraging success, and demonstrates one of the selective pressures that may have been responsible for the evolution of the capacity of ambush predators to consume very large meals as snakes that are able to ingest more energy are more likely to reproduce.

7.4.1 Feeding

Observations of feeding suggest that large *Bitis schneideri* do not exclude small meals from their diet. Arnold (1993) reviewed studies that have investigated snake-size prey-size relations, and found that the majority of species showed an ontogenetic shift in lower limit of prey size. Arnold (1993) argued that for marginal prey to be valuable to a predator, the energetic gains from the meal (however small) need to outweigh the risks of consuming it. Shine (1977) proposed that relatively small prey were still valuable to snakes from three genera of Australian elapids because the snakes were venomous and thus able to limit the costs associated with consuming prey. The use of venom by *B. schneideri* could similarly explain the presence of relatively small prey items in the diet of large individuals. Additionally, in ambush foraging snakes such as *B. schneideri,* low metabolic expenditure resulting from reduced activity and physiological adaptations to infrequent feeding (Secor & Nagy, 1994; Secor & Diamond, 1998), the overall energetic expenditure is low relative to more actively foraging snakes, and thus the cost of locating and capturing such marginal prey is reduced. Studies of species that do exhibit ontogenetic shifts in minimum prey size have attributed such changes to ontogenetic shifts in habitat use or morphological limitations that prevent large snakes consuming small prey (Arnold, 1993). Field observations suggest no ontogenetic shifts in habitat use in *B. schneideri,* limiting the effect of habitat on prey size availability. Moreover, even adult *B. schneideri* are capable of consuming the smallest vertebrates in the prey community, suggesting that there are no morphological constraints to feeding on small prey items.

I found no evidence that *B. schneideri* consumes arthropods, as do many other small-bodied viperids (Phelps, 2010) including several arid-adapted African species (Barlow et al., 2009). The most abundant invertebrates on the study site were Tenebrionid beetles, which have thick chitinous exoskeletons that increase the cost of digestion and probably make ingestion of them unprofitable (Chen et al., 2004).

Feeding behaviour during winter is often restricted in ectothermic vertebrates such as snakes (Mori et al., 2002). The arid coastal region that *B. schneideri* inhabits is tempered by the cold Benguella current, and as such experiences reduced seasonality (Robinson & Seely, 1980). The feeding behaviour that I observed during winter is thus likely a result of the mild winters that occur in the region, and possibly, the digestive advantage resulting from the use of venom at low temperatures (but see Chu et al., 2009). The capacity to feed year-round has important implications for energy intake, and may be the factor that allows *B. schneideri* to breed annually (Chapter 6).

Estimated prey encounter rates resulted in few captures and thus low mean energy intake. Secor and Nagy (1994) estimated energy expenditure for *Crotalus cerastes* as 38.6 $kJ.kg^{-1}.d^{-1}$. If I assume similar energy expenditure for *B. schneideri*, then a 15 g snake would need to consume approximately 210 $kJ.yr^{-1}$ in order to survive. This estimate would suggest that the measures of prey encounter rates are artificially low (only half of the energy needed to sustain an individual would be available), most likely the result of prey animals avoiding pitfall traps more easily than they avoid ambushing snakes.

7.4.2 Advantages of consuming very large meals

My simulations showed that mean energy intake for snakes that had the capacity to capture very large meals was always higher than the mean energy intake of snakes that did not. Moreover, the relative advantage of consuming very large meals was dependent on the shape of the energy availability distribution and was independent of prey encounter rates. Based on the shape of the energy availability distribution for the prey community, snakes that had the capacity to consume very large meals had a 30% improvement in energy ingestion.

The relationship between energy surplus and fitness is complex, making it difficult to quantify the biological significance of the increased energy intake associated with the capacity to consume very large meals. However, several studies have linked patterns of prey abundance and thus food availability with reproductive output (Shine & Madsen, 1997;

Madsen & Shine, 1999a,b, 2000) suggesting that even relatively small differences in prey availability can translate into changes in reproductive output. Thus the capacity to consume very large meals is likely to represent a strong competitive, and therefore selective, advantage to snakes that have such a capacity.

There are undoubtedly costs associated with consuming very large meals (as well as costs associated with the morphology required to consume very large meals), and these should be weighed against the energetic advantages of increased energy intake. Larger prey items are associated with increased handling time which may expose snakes to predators, limit locomotion, and utilize time that may be spent on other activities. While increased handling time is likely to influences snake foraging behaviour by influencing the cost-benefit ratio of particular prey items, a single very large meal may fulfil an individual's annual energetic maintenance requirements.

This study demonstrates that the energy gain to an ambushing *B. schneideri* is governed by the relative abundance of prey types, and their respective energy contents. Moreover, the availability of meals derived from these factors suggests that very large meals are encountered only rarely by ambushing snakes, but that if they are consumed, provide the predator with a large energy bonanza. Given that large energy surplus is likely to result in increased fecundity it is unsurprising that vipers have evolved the capacity to consume very large meals.

CHAPTER 8

ASSESSING THE THREAT OF AVIAN PREDATION ON A SMALL VIPERID SNAKE

This chapter has been published as Maritz, B., and Scott, S. L. 2010. Assessing the threat of avian predation on a small viperid snake. African Zoology. 45:309-314.

Abstract – Predators are important because they influence survival rates, population density, and behaviour of prey species. However, assessing the predation pressure facing a particular species is difficult when that species faces a suite of predators. We aimed to characterise the suite of avian predators that are likely to feed on the Namaqua Dwarf Adder, *Bitis schneideri*, and used field surveys to assess their relative abundance. We used literature records to map the feeding preferences of avian species, and point counts to estimate relative abundance. Finally, we produced an index of Relative Predatory Pressure (RPP) to assess the relative importance of each avian species as predators. We counted 490 individual birds from 30 species during 39 point counts. A cluster analysis of similarity between diets produced a dendrogram that we split into three functional groups: specialist predators, generalist predators, and non-predators. Specialist predators and generalist predators made up a total of 10.6 % of the entire community by abundance. Generalist predators are likely to be the most important predators of Namaqua Dwarf Adders. We also noted an increased abundance of anthropophylic species outside of our study site and suggest that anthropogenic areas could provide regions of increased predation pressure on small vertebrates.

8.1 Introduction

Predators play an important role in regulating prey populations (Greene, 1988; Lima, 1998; Meunier et al., 2000; Newton, 2003; Begon et al., 2006), activity patterns (Greene, 1988; Lima & Dill, 1990; Webb & Whiting, 2005), and driving anti-predatory behaviour and mechanisms (Greene, 1988; Lima & Dill, 1990). In nature, most prey species encounter multiple predators (Sih et al., 1998). Accordingly, understanding the range of predators that feed on individuals of a particular prey species is essential for understanding factors that

regulate populations and influence the evolution of anti-predatory behaviours (Sih et al., 1998). Despite its value, few data are available regarding predation on African snakes. Most records are represented by anecdotal or isolated reports (e.g., Alexander & Maritz, 2010), from the dissection of museum specimens (Louette & Herroelen, 2007), or from the analysis of faecal pellets (Macdonald & Dean, 1984; Simmons et al., 1991; van Zyl, 1994).

Small vertebrates are often subject to predation by a large and diverse suite of predatory species ranging from other vertebrates to large invertebrates (Greene, 1988; Andrews & Gibbons, 2005). However the relative abundance of these predators and their propensity to feed on a particular prey species will influence the degree of predation pressure that they exert on the prey species (Greene, 1988). For example, an abundant generalist predator may have little effect on a prey species, whereas an uncommon specialist predator can exert a strong effect on the prey population (Paine, 1974). In this study we investigated the potential predatory pressure that avian predators place on a population of a small viperid snake, *Bitis schneideri.*

The Namaqua Dwarf Adder (*Bitis schneideri*) is a desert adapted viperid snake, endemic to the west coast of southern Africa (Broadley, 1990; Branch, 1998). Individuals are small (100 mm to 285 mm total length), and abundant within the Sandveld bioregion that they inhabit (B. Maritz, unpubl. data). While Branch (1998) describes the species as nocturnal, our unpublished activity data indicate that individuals are primarily diurnal with limited nocturnal movement. *Bitis schneideri* is listed as Vulnerable by the IUCN on the basis of habitat destruction from diamond mining activities and illegal collection for the pet trade (Branch, 1988; World Conservation Monitoring Centre, 1996). Since predators play an important role in regulating population sizes, understanding the predatory pressure facing a threatened species can help inform conservation actions.

Individual *B. schneideri* face predation risk from a vast array of predators including birds, mammals (e.g. Yellow Mongoose, *Cynictis penicillata* and Suricate, *Suricata suricatta*), other reptiles (e.g. Cape Cobra, *Naja nivea*), and potentially even large invertebrates (e.g. Namaqua Baboon Spider, *Harpactira namaquensis*), all of which are syntopic with *B. schneideri* within our study site. We chose to investigate avian predatory pressure because birds are likely the most important predatory group, on account of their relative abundance and ecological diversity (Hockey et al., 2005). Moreover, the relative ease with which they can be surveyed

and quantified means that their predatory significance can be more accurately estimated than is the case for other taxa.

Using the available literature we compared the diet of all detected bird species at our study site during the summer activity period to ascertain which species are likely to feed on Namaqua Dwarf Adders. We then surveyed birds on the site to calculate relative abundance of the candidate predatory species. Finally, we used the data from these two analyses to produce an index of Relative Predatory Pressure (RPP) posed by avian predators of *B. schneideri*.

8.2 Methods

All data were collected during the austral summer along coastal dune fields on the farm Noup, Northern Cape Province, South Africa (30°08′ S; 17°12′ E). Noup forms part of Namaqualand Mines and the De Beers Diamond Route, however all dune habitats are relatively pristine. The study site is approximately rectangular in shape and covers 480 ha. The study site was selected to meet the criteria of ongoing research on the ecology of *B. schneideri*. The area is comprised primarily of recent calcareous aeolian sands that form semi-vegetated longitudinal dunes (Desmet, 1996; Desmet & Cowling, 1999). Vegetation is succulent or sclerophyllous as is typical for Sandveld habitats along the coast (Mucina & Rutherford, 2006). The region receives 50 - 150 mm rainfall per annum, and coastal fog is frequent (Cowling et al., 1999). More than 60% of annual rainfall falls during winter (Desmet, 2007). Temperatures are cool, ranging from a mean temperature of 14.3 ºC in winter to 18.2 ºC in summer (Desmet, 2007).

We obtained dietary data from the literature (Hockey et al., 2005 and references therein) for all bird species that we observed at the study site during extended field work over the austral summers since September 2007. We scored each species for the presence of insects, arachnids, molluscs, reptiles, fish, amphibians, birds, mammals, fruits, seeds, nectar, foliage, or carrion in their diet. We calculated the Euclidean distances between the diets of each species and plotted the resultant dendrogram using Statistica v. 6 (Statsoft Inc., 2001). We subjectively defined three primary feeding groups on the basis of dietary overlap, namely specialist predators, generalist predators, and non-predators.

We sampled the avian community at our study site from 15 - 29 December 2009. In total we conducted 39 point counts of 15 min each to sample the species richness and relative abundance of birds within the study site. Surveys were conducted daily during the early morning and late afternoon to sample birds during different periods of activity. During point counts it is often necessary to account for the reduction in detectability with increasing distance from the observer (Reynolds et al., 1980). However, our study habitat was relatively sparsely vegetated allowing us to comfortably detect birds from long distances. Accordingly, we limited our counts to birds within 100 m to account for the relatively open habitat and the low density of birds in the arid environment. Prior to each survey we identified landmarks approximately 100 m from our observation point. We included all individuals that were seen or heard. Birds identified on the basis of calls were only included if both observers agreed that the calling individual(s) were within the designated 100 m radius. To minimize the likelihood of duplicating counts, points were sampled at least 200 m apart.

On the basis of our literature survey and our avian community survey we constructed an index of Relative Predatory Pressure (RPP), calculated as $RPP = (RA \times G)/G_{max}$, where *RPP* is Relative predatory pressure that ranges from 0 to 1, *RA* is the relative abundance of a particular species, *G* is a defined guild-specific integer scored as 0 for non-predators, 1 for generalist predators, and 2 for specialist predators, and G_{max} is the highest value for *G* in the analysis. Our index of RPP is similar to that described by Gunzberger & Travis (2004), but differs in that we did not have access to predator specific information on consumption of Dwarf Adders. In our analysis G_{max} equalled 2, however this assumes that a specialist predator consumes twice as many Dwarf Adders as a generalist predator. Data to support this assumption were not available to us. However, we tested sensitivity of our analysis by varying G_{max} between 1 and 10 and comparing the rank order of the species using Spearman Rank Order Correlation, and found that our results and conclusions were supported (a generalist predator achieved the top rank) up to a G_{max} equal to approximately four which we think is an ecologically reasonable assumption (Gunzberger & Travis, 2004).

8.3 Results and Discussion

Field observations on the study site yielded 64 species that we included in our feeding analysis (Fig. 8.1). Avian species likely to feed on Namaqua Dwarf Adders (specialist predators + generalist predators) clustered together as distinct from non-predators (Fig. 1).

Within this group specialist predators (13 species) were distinct from generalist predators (8 species) (Fig. 8.1). The remaining species (43 species) were classified as non-predators, though they included two subsets of birds that have exceptionally been noted as including small reptiles in their diets (Fig. 8.1).

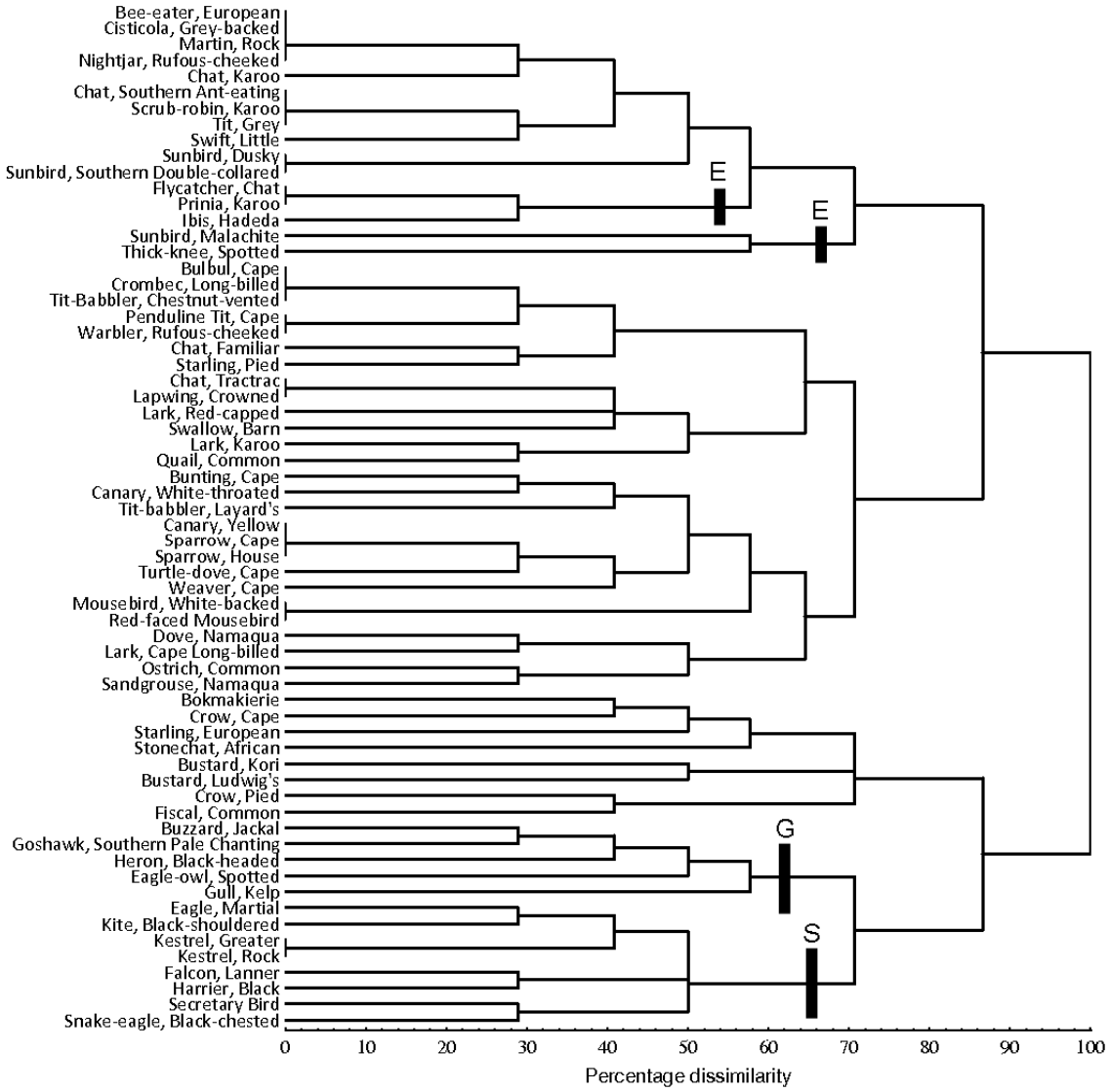


Figure 8.1: Dendrogram showing Euclidian dissimilarity in diet among 64 species of birds observed on our study site during summers of 2007, 2008 and 2009. Most species are non-predators, however groupings of generalist predators (G), specialist predators (S), and the two cases of exceptional cases (E) are shown.

Surveys of the avian community yielded 490 individual records representing 30 species. Non-predators were most abundant (the 5 most abundant species were non-predators and

comprised 50.4% of all individual birds by abundance; Fig. 8.2). Specialist predators make up a relatively small proportion of the avian community by abundance and were represented by only three species during our survey (Black-headed heron + Southern Pale Chanting Goshawk + Greater Kestrel = 1.8%). Generalist predators, primarily Bokmakierie and Common Fiscal, made up 8.8 % of all individual birds detected during our surveys.

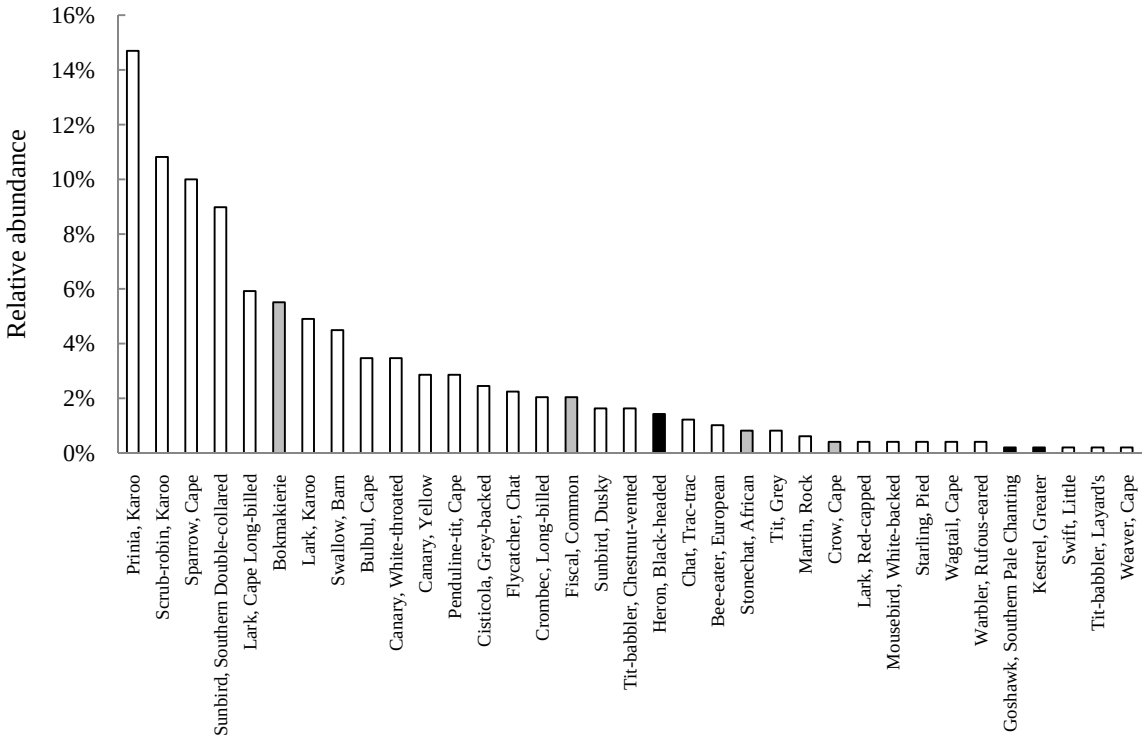


Figure 8.2: Relative abundance of all bird species detected during surveys on our study site from 15 - 29 December 2009. Black columns represent specialist predators, grey columns represent generalist predators, and white columns represent non-predators.

In our study system, a relatively large proportion of recorded avian species are likely to include Dwarf Adders in their diets. In our analysis of dietary composition, 13 species (20.3%) clustered as specialist predators, while an additional 8 species (12.5%) clustered as generalist predators that could include Dwarf Adders, especially juvenile snakes, in their diet. Thus 32.8% of the avian species known to occur in the area are likely to include Dwarf Adders in their diet.

Relative Predatory Pressure (RPP) indicated that Bokmakierie were likely the greatest avian threat to Namaqua Dwarf Adders, followed by Black-headed Heron and Common Fiscal

(Table 8.1). Despite their small size, African Stonechat scored relatively high (RPP = 0.007) because of its relative abundance and the inclusion of vertebrates (including fish and reptiles – Keith et al., 1992) in its diet. Despite making up a significant proportion of the species community, specialist predators appear to be relatively scarce in abundance, as predicted by trophic theory (Begon et al., 2006). The estimated relative abundance of all specialist predators during our surveys was 1.84 %. Thus, while such typical predators are often expected to form the major predatory pressure on particular species (Broadley, 1990), their relative abundance and RPP indicates that they may be less important in terms of individual prey items consumed over a period of time.

Table 8.1: Relative predatory pressure (RPP) for the seven likely predators detected during our surveys. RA = Relative abundance, G = Feeding guild score.

Species	***RA***	***G***	***RPP***
Bokmakierie (*Telophorus zeylonus*)	0.055	1	0.028
Heron, Black-headed (*Ardea melanocephala*)	0.014	2	0.014
Fiscal, Common (*Lanius collaris*)	0.020	1	0.010
Stonechat, African (*Saxicola torquatus*)	0.014	1	0.007
Crow, Cape (*Corvus capensis*)	0.004	1	0.002
Goshawk, Southern Pale Chanting (*Melierax canorus*)	0.002	2	0.002
Kestrel, Greater (*Falco rupicoloides*)	0.002	2	0.002

We suggest that the major avian predatory pressure facing Dwarf Adders is likely from generalist predators that feed on Dwarf Adders opportunistically. Our cluster analysis indicates that 8 species that occur in the study area can be included in this group, and our survey data suggest that these species make up 8 % of all birds occurring in the area by abundance (Fig. 8.1).

Our survey of the avian feeding literature records yielded several surprising feeding records. These include the inclusion of small reptiles (primarily lizards) in the diets of Karoo Prinia (Frazer, 1987) and Malachite Sunbird (Starck, 1900). While these records are for small lizards, and these species could potentially feed on neonate Namaqua Dwarf Adders (110 mm, 2.5 g), we designated these species as non-predators, choosing to interpret their observations as exceptional cases. Nonetheless, the potential threat posed by species that are

abundant (Karoo Prinia was the most abundant species during our surveys) but rarely feed on target taxa could be very important and should be investigated.

Although we did not quantify the abundance of bird species along major roads, power lines and towns in the area, many of the anthropophylic species that are common in these areas (Cape Crow, Pied Crow, and European Starling) were species that we included as potential predators of *B. schneideri*. The prevalence of raptors along power lines is well known (Ledger & Hobbs, 1999; Meunier et al., 2000; Landman et al., 2001; Lasch et al., 2010), and Greater Kestrel, Rock Kestrel, and Southern Pale Chanting Goshawk are common along the major road and power line that runs nearby (*Pers. Obs.*), yet made up a relatively small proportion during our surveys, away from the roads and other anthropogenic areas. It is therefore likely that anthropogenic areas are likely to produce artificially inflated risk of predation on Dwarf Adders from anthropophylic bird species.

While specialist predators do impose population level effects on Dwarf Adders, we suggest that generalist predators and opportunists may impose a greater influence on snake populations and behaviour. Our data has shed light on the risk that Dwarf Adders face from avian predators in the wild and provides a valuable framework for assessing future behavioural ecology investigations in *Bitis schneideri*. We also think that our approach provides a valuable tool for dealing with the difficulties associated with estimating predation pressure.

8.4 Acknowledgements

We would like to acknowledge Joshua Hocepied and Bruce Wessels who assisted us during fieldwork. Dudley and Aletta Wessels are thanked for accommodation and continued support. This project would not be in place without the support of Namaqualand Mines and Ernst Oppenheimer and Sons. Andrew McKechnie and two other reviewers made valuable comments on a previous draft of this manuscript.

CHAPTER 9

CRITICALLY ASSESSING CHANGES IN CONSERVATION STATUS: THE VALUE OF HOLISTIC ORGANISMAL BIOLOGY

9.1 Introduction

A species can be viewed as a house built from playing cards where each card in the species' card-house represents a facet of its biology. The structural integrity of a house of cards is dependent on how stress is distributed through the house. Similarly, the persistence of a species is the result of the interaction of the different facets of the species' biology. Disturbance of one card may, or may not, compromise the structural integrity of the house. Similarly, introduce a perturbation that acts to significantly influence a facet of the species' biology, or its interaction with other facets, and there is a risk that the integrity of the species will be compromised, resulting in changes in population size, and potentially extirpation or even extinction. Not all perturbations influence all facets of biology, just as physical removal of a card or a light breeze will have different influences on the house.

For species that are of conservation concern, effective conservation requires an understanding of their life history (Sæther et al., 1996; Greene, 2005). However, such basic information is lacking for most species, hindering effective conservation and management (Greene, 2005). It is only through the development of a holistic understanding of the biology of the threatened species, and the resultant capacity to predict the response of that species to perturbation, that effective conservation management can be developed.

Threatened species are not evenly distributed across the globe. A disproportionate number of threatened species occur in politically unstable regions, and the biology of most of those organisms are generally very poorly understood (Hanson et al., 2009). Moreover, not all organisms have been given equal attention by scientists. Reviews of the literature regarding the ecology of snakes, for example, have demonstrated that snakes have historically been drastically under-represented by ecological studies (Shine & Bonnet, 2000), and that studies on snake ecology are more difficult to publish than those investigating the ecology of other vertebrate taxa such as birds and mammals (Bonnet et al., 2002a).

Recent work describing global declines in reptile populations in general (Gibbons et al., 2000), and snake populations specifically (Reading et al., 2010), have highlighted the conundrum of trying to conserve what we do not properly understand. The conservation of African snakes provides a clear example of this issue - poorly studied organisms that inhabit poorly studied environments in which the response to proximal threats are unknown. African snakes are diverse (Broadley, 1983; Greene, 1997; Branch, 1998), very poorly understood (Branch, 1988), phylogenetically distinct (Cadle, 1994), and appear to differ ecologically from snake faunas in other parts of the world (Janzen, 1976). Additionally, political instability has limited biologists from easily accessing many parts of the continent, hindering research into the biology of these and other species.

Branch (1988) has pointed out that even in southern Africa, with its relatively well-developed infrastructure and relative political stability, little research on snake ecology has been conducted. The situation has not changed appreciably since this statement was made. The work on *Python natalensis* (Alexander, 2007), *Hemachatus haemachatus* (Alexander, 1996), *Bitis gabonica* (Bodbijl, 1994; Linn et al., 2006; Warner, 2009), and *Psammophis* and *Psammophylax* (Cottone, 2007; Cottone & Bauer, 2010) stand out as the only field ecological research to be conducted on snakes in southern Africa during the last two decades. Without exception, all other knowledge of snake ecology is derived from the dissection of museums specimens (e.g., Shine et al., 1998; Keogh et al., 2000; Webb et al., 2001; Ineich et al., 2006; Shine et al., 2007), anecdotal observations (e.g., Marais & MaGahey, 2010; Visser, 2010; Warner & Kyle, 2010; Deans, 2011), or community-wide surveys (e.g., Maritz & Alexander, 2007; Masterson et al., 2007; 2008).

Bitis schneideri has long been considered to be of conservation concern (McLaughlin, 1978; Branch, 1988; World Conservation Monitoring Center, 1996). Recently, however, the species has been listed as Least Concern (Turner & Maritz, In press) as a result of more information on its distribution and ecology, as described in this thesis. Turner & Maritz (In press) explicitly state that the species is now “considered Least Concern, pending analyses of population size and threats.” In this chapter, I critically assess this change in conservation status by synthesizing recent work on the species, and interpreting the threats facing *B. schneideri* in the light of our improved understanding of its ecology.

9.1.1 *Ecology of the Namaqua Dwarf Adder*, Bitis schneideri (Fig. 9.1)

Bitis schneideri is a species of small-bodied viperids. Maritz & Alexander (In Press-a) hypothesise that the selective advantage of being able to bury into sandy substrates has resulted in the extreme small body size in the species. Small body size has two important implications for the biology of the species. Firstly, small body size provides a physical constraint to the number of offspring that a snake can produce. Secondly, it negates the need for feeding specialization among predators and thus is likely to widen the suite of predators capable of preying on *B. schneideri*.

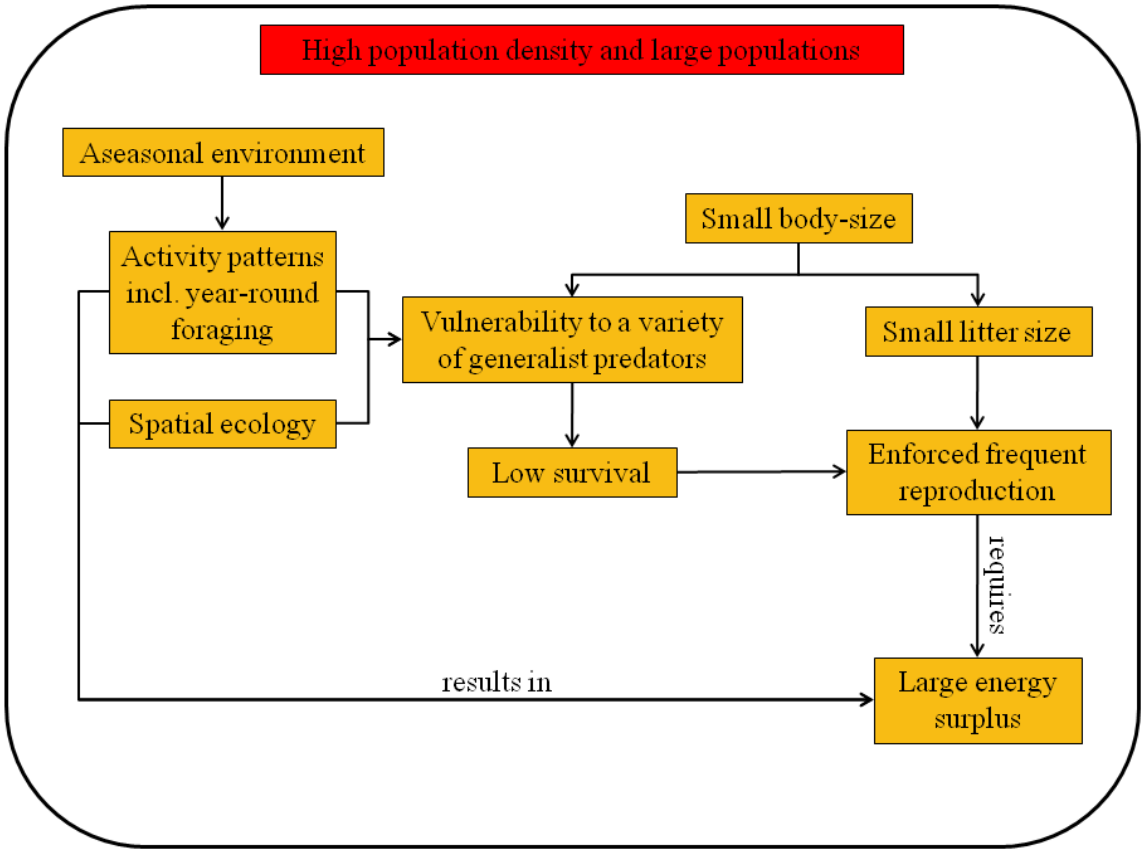


Figure 9.1: The interaction of the various aspects of *B. schneideri* ecology. Direction of arrows designates the direction of influence.

Being vulnerable to a wide suite of predators is likely to result in increased predation pressure and may be the reason that *B. schneideri* experiences low levels of survival. Bouts of movement are strongly associated with increased predation risk among relatively sedentary and cryptic animals (e.g., Alexander & Maritz, 2011). Thus it is unsurprising that cryptic ambush predators minimize predation risk by reducing the distance and frequency of

movement. An additional driver of reduced movement is energy savings. Ambush predators have low energy requirements because of physiological and behavioural mechanisms that act to reduce energy expenditure (Secor & Diamond, 1998). Moreover, many ambush-foraging snakes tend to move shorter distances and less frequently than actively foraging snake species (Secor, 1994). Risk of predation while moving and the energetic costs of that movement have likely been important in shaping of the sedentary lifestyle exhibited by *B. schneideri* and as a result predispose the species to being vulnerable to habitat fragmentation.

Low survival has an additional important implication for *B. schneideri* biology: when combined with small litter size, low survival dictates that *B. schneideri* reproduce frequently. This condition is unusual among viperid snakes as most species reproduce only every second or third year (Seigel & Ford, 1987). An important constraint that appears to prohibit viperids from breeding frequently is the low energy intake associated with ambush predation (Seigel & Ford, 1987). Thus an important ecological trait that allows *B. schneideri* to persist is the capacity to continue to feed year-round. This is probably a fortuitous consequence of the mild winter conditions that prevail along the coast in this region, moderated by the Benguella current. However, Maritz & Alexander (Submitted-a) demonstrated that activity, and probably other aspects of biology, are constrained to days with suitable weather conditions during winter, suggesting sensitivity to changes in the frequency at which those weather conditions occur.

Finally, Maritz & Alexander (Submitted-b) demonstrated that Dwarf Adders occur at high population densities and accordingly, have large population sizes. This aspect of *B. schneideri* biology provides the context in which all aspects of biology need to be interpreted, as large populations tend to be more buffered against perturbations.

9.2 Threats

Conservation assessments for *B. schneideri* have highlighted two primary threats to the species. These include habitat loss, primarily as a result of mining activities, and illegal collection for the pet trade (Branch, 1988; World Conservation Monitoring Centre, 1996; Turner & Maritz, In press). Additionally, the Succulent Karoo is expected to experience significant changes in climate in the future (Rutherford et al., 2000).

9.2.1 Habitat loss/transformation

Habitat loss and transformation are among the most significant threats facing biodiversity globally (Brooks et al., 2002). Recently, Reading et al. (2010) proposed that global declines in snake populations are likely to be linked to habitat loss, among other threats. Habitat loss and transformation are likely to influence a population in two important manners. Firstly, reduction in total available habitat is likely to reduce the overall population size through reduction in the absolute availability of resources, making the population more vulnerable to extinction. Large population size can provide resilience to extinction by allowing the population to recover from population crashes. For species that exhibit large fluctuations in population size associated with variable environmental drivers or stochasticity, the capacity to recover from large reductions in population size is essential. Although long-term population data are not available, I suspect that *B. schneideri* populations probably exhibit large fluctuations in population size because of variability in the suitability of conditions (including fluctuations in prey availability, predator pressure, and habitat structure) and because they have low survival rates (apart from low fecundity, *B. schneideri* is a typical *r*-selected species). Large population size may thus be essential for buffering such fluctuations.

The second way that habitat transformation may negatively impact the conservation *B. schneideri* is the fragmentation of populations due to habitat degradation or the formation of barriers. Habitat fragmentation has been implicated as an important threat to biodiversity (Meffe & Carroll, 1997) and is known to result in genetic effects associated with inbreeding depression as well as the isolation of small populations vulnerable to extirpation (Templeton et al., 2000). The impact of habitat fragmentation is strongly related to dispersal ability, with species that exhibit low dispersal ability being vulnerable to even small barriers. Clarke et al. (2010) demonstrated significant genetic structuring in a population of *Crotalus horridus* as a result of habitat fragmentation stemming from the development of the road network. *Bitis schneideri* is known to display a sedentary lifestyle, low dispersal ability (Maritz & Alexander, In Press-b) and strong habitat associations, suggesting that even moderate habitat fragmentation could have important impacts on gene-flow and isolation of sub-populations, especially given the fragmented nature of suitable habitat.

Minimum viable population size has been a much-debated aspect of conservation biology for decades (Flather et al., 2011). From a species perspective, the IUCN has defined the threshold for extinction concern as 10 000 mature individuals in the global population (IUCN, 2001).

At population densities of 8 ha^{-1}, the primary dune cordon on which my work was performed (of which my study site forms only part) is likely to host a population in excess of 20 000 individuals, and is thus large enough to be considered Least Concern by IUCN criteria. However, species that naturally exist under high population densities may depend on those high densities to avoid extirpation. Passenger pigeons (*Ectopistes migratorius*) were once abundant, but reductions in population size from hunting apparently reduced population size below a threshold and resulted in the extinction of the species (Halliday, 1980).

9.2.2 Illegal collection for pet trade

The illegal collection of snakes for the pet trade has been cited as a threat to *B. schneideri* (Branch, 1988; World Conservation Monitoring Center, 1996; Turner & Maritz, 2011). Because of the nature of illegal trade, the extent and intensity of illegal collection of reptiles in Africa is unknown (Schlaepfer et al., 2005). The primary impact of illegal collection is a reduction in population size. However, secondary effects such shifts in sex ratios or population structure can also result in negative impacts on wild populations (Milner et al., 2007).

Several life history traits have been identified as increasing vulnerability to over-harvesting. Primary among these are species that are long-lived and mature slowly, occur at low population densities, are not highly fecund, or form dense aggregations during times of the year and are thus easy to collect (Reed & Shine, 2002; Webb et al., 2002b). *Bitis schneideri* has none of these attributes, and it is thus likely that the species would be resistant to all but the most intensive collecting impacts.

Given the dependence of population persistence on frequent reproduction in *B. schneideri* (Chapter 6), changes to population structure, and particularly sex ratios may have negative impacts on wild populations. However, Maritz & Alexander (Submitted-b) did not detect significantly different detection probabilities for male and female snakes, suggesting that the collection of individuals is unlikely to bias particular sexes. Biased collecting favouring adult snakes over less detectable juvenile snakes (Maritz & Alexander, Submitted-b) will probably simulate a minor increase in general predation pressure, and as such not have a large impact on population dynamics.

9.2.3 Climate change

Climate change is predicted to have significant impacts on the Succulent Karroo Biome (Rutherford et al., 2000). In general, climate models predict increased mean temperatures, increasing aridity, and reduced reliability of rainfall. However the difficulties associated with down-scaling broad-scale climate model predictions to the local scales at which those changes influence individuals and populations limits prediction of proximal responses of species to changing environments (Wiens & Bachelet, 2010). Moreover, population-level responses to changing environments are likely to be mediated through both mutualistic and antagonistic interactions with other species, making accurate prediction of those changes challenging (Hulme, 2005). However, any assessment of conservation risk that does not include the threat of climate change is short-sighted. Here, I present my expectations for some of the major environmental changes associated with climate predictions.

Maritz & Alexander (Submitted-a) showed that activity did not cease during winter, but was more strongly associated with suitable (generally warmer) environmental conditions during this season. I proposed that it is the continuation of activity, and particularly feeding, during winter months that allow individuals to reproduce frequently and thus persist in the face of low clutch size and low survival. Increased temperatures during winter months would likely result in a greater number of days suitable for feeding, and as such have the potential to impact *B. schneideri* reproductive output, directly influencing population size.

Warming may not, however, have only positive influences on snake populations. For example, our unpublished data suggest that exposed sandy patches reach lethally high temperatures (> 42 °C) for much of the day during summer months, excluding snakes from this component of the habitat. An increase in day-time temperatures could exacerbate this problem - longer periods of lethally high temperatures for a greater number of days annually. Additionally, if increased temperatures are associated with a decrease in vegetation cover, then the proportion of habitat remaining available to *B. schneideri* could be reduced.

Secondary impacts of climate change on *B. schneideri* biology are even more difficult to predict than primary impacts. Two important potential secondary impacts include changes in the composition and abundance of predator and prey communities. Because *B. schneideri* is a generalist predator that does not appear to display dietary preferences, a change in the prey community composition is unlikely to have a negative influence. However, because of the apparent link between food intake and reproductive output, a reduction in overall prey

abundance may well have severe negative impacts on snake population size by reducing population recruitment (Chapter 7). Similarly, predicting the response of *B. schneideri* populations to changes in predator communities is difficult. Changes in predator communities are known to have significant destabilizing impacts on food-webs (Prugh et al., 2009). Additionally, small body size, low survival, and diverse suite of predators (Maritz & Scott, 2010), suggests that predation is likely to play an important role in governing population size. However, Maritz & Scott (2010) also demonstrated that among avian predators, abundant generalist are likely to be have a greater impact on *B. schneideri* population size than less abundant specialist predators. Vulnerability to generalist predators suggests that changes in predator community composition are unlikely to have major impacts on mortality rates. However, overall changes in predator abundance may have significant impacts on mortality rates.

Finally, changes in climatic conditions may have impacts on prevailing on-shore winds. The semi-vegetated dunes that form the primary habitat of *B. schneideri* are aeolian in origin, and as such, changes in the wind could impact dune structure, and potentially result in the loss of suitable habitat. However, such changes are very difficult to predict accurately.

9.3 Discussion

This review suggests that the change in conservation status of *Bitis schneideri*, from Vulnerable to Least Concern, is appropriate, and that *B. schneideri* is not facing significant risk of extinction in the near future. The primary biological factor that ameliorates against extinction risk is large population size and population density. Thus the combination of very large global population size, geographic range, and no evidence of population declines excludes the species from all threat categories recognised by the IUCN (IUCN, 2001). However, this work reveals low dispersal ability combined with habitat fragmentation as the most important threat to *B. schneideri*. Additionally, impacts associated with climate change are likely to be both positive and negative through increasing the availability of suitable weather conditions for activities such as foraging, or through reducing vegetation cover and food availability respectively. So although the risk of extinction for *B. schneideri* is low, the dynamic nature of how threats and species interact, and the low confidence associated with climate change predictions means that the species should not be ignored by conservation biologists.

Critical assessment of conservation status changes are an important step in effective conservation planning. My approach to the reassessment of the conservation status of *B. schneideri* provides a valuable framework for how such reassessments should take place. And while my research has undoubtedly provided a strong foundation for understanding the biology of *B. schneideri*, and makes the species one of the best ecologically understood species in Africa, there are still some important gaps in the knowledge that need to be quantified. These include:

1) Reproductive cycles, including the timing of sperm and egg production will provide a better understanding of life-time reproductive output.
2) Explicit quantification of energy intake, energy expenditure, and the subsequent effect of energy surplus on reproductive output would be informative and clarify the impacts of changing food availability and foraging success on population dynamics.
3) Measurement of long-term fluctuations in population size would provide insight into population resilience.
4) The relative contribution of top-down (predator-controlled), and bottom-up (resource-limited) regulation of population size would inform our understanding of population dynamics.
5) The genetic effects associated with isolation of populations through habitat fragmentation will allow for more accurate assessment of the risks associated with habitat fragmentation.
6) The taxonomic status of the species and more specifically the status of Namibian populations.
7) More intensive and comprehensive mapping of the distribution including the mapping of source and sink areas will help to understand the degree of fragmentation in the population.

The approach that I have adopted is not novel. Biologists have, for many years, called for holistic approaches to understanding the vulnerability of organisms to extinction. Greene (2005) explicitly highlights the role of organismal biology as a central focus of conservation biology. However, in the context of Africa, and the conservation of poorly understood organisms, the approach that I have used and outlined here, and ideally including the facets listed above, should form the protocol for how single-species conservation should be approached.

Developing an understanding of the biology of a species goes beyond effective conservation management. Population persistence governs patterns of geographic distribution, and range edges are defined by areas where a species cannot persist. Given that the persistence of a species is governed by the interactions of the different facets of the biology of an organism, my approach is likely to highlight the aspects of an organism's biology that allow its persistence in certain areas, while excluding it in others.

In southern Africa there are several snake species to which my approach, and indeed my data, could be immediately applied. Both *B. armata* (Endangered) and *B. albanica* (Critically Endangered) are small vipers that are very poorly understood and face severe risk of extinction in the near future (Bates et al., In Press). Studies quantifying and characterizing the biology of these species will not only aide directly in the conservation of those species, but also help to clarify issues of conservation at higher taxonomic levels. The genus *Bitis* contains several small-bodied, restricted-range species, several of which are of conservation concern. Ascertaining the factors that have lead to members of the genus being susceptible to environmental perturbation can have important implications for the identification of life history traits that characterize species of conservation concern.

The African snake fauna is diverse, poorly documented, poorly understood, and given growing human populations, increasingly imperilled. Yet research investigating the ecology of these charismatic and ecologically important animals remains conspicuous by its absence. However the potential for such research is an opportunity waiting to be exploited. Hopefully a growth in African snake ecology, mirroring the growth of the science globally, is on the horizon.

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