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Conservation Biology of the Gaboon Adder (*Bitis gabonica*) in South Africa

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A dissertation submitted to the School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa in fulfilment of the requirements of the degree of Masters of Science.

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ABSTRACT

From 2005-2007, I studied the ecology of *Bitis gabonica*, a terrestrial forest viperid that occurs in subtropical northeast extremes of South Africa. I monitored ten individuals (six males and four females) using radiotelemetry inside the iSimangaliso Wetland Park in KwaZulu-Natal. I used two different home range estimators to analyze space use among individuals; minimum convex polygons (MCPs) and kernel density contours (KDs). MCPs averaged 28.58 ha (42.48 ha for males, 7.72 ha for females) and ninety-five percent kernel density contours (KDs) averaged 28.92 ha (42.65 ha for males, 8.32 for females). Fifty percent KDs (core areas of activity) averaged 6.74 ha, with the mean male core activity centre almost five times greater than that of females. Telemetered *B. gabonica* were highly sedentary, especially during winter when individuals remained at single localities for extended periods (max. 87 days). Activity peaked for both sexes at the onset of the breeding season, with individuals averaging a movement distance of 598 m during March.

At sites where telemetered *B. gabonica* were observed, I measured a suite of sixteen critical habitat variables and then used MANOVA to test for differences among habitat characteristics for several different categories (season, sex and habitat selection). *Bitis gabonica* habitat preferences were strongly influenced by season, with individuals selecting open-canopied areas during cooler months, presumably because the forested habitat individuals utilize the rest of the year is not adequate for the species' thermoregulatory requirements during winter. Female *B. gabonica* used slightly less shrubby microhabitats than males. The variability found between *B. gabonica* sites and random sites was primarily explained by features that constitute the understory, with snake sites having denser understory structures and being located closer to woody vegetation. This type of "thicket" microhabitat is important for the protection, thermoregulation and food acquisition requirements of Gaboon Adders.

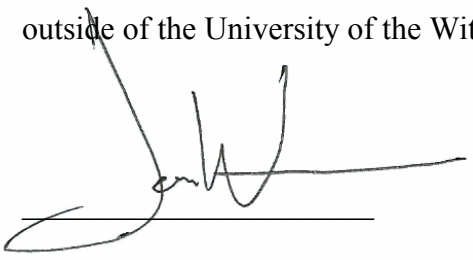
Among telemetered *B. gabonica*, feeding activity varied between seasons, with individuals spending long periods of time at single localities in an ambush position, especially during summer. Snakes exhibited strong ambush site fidelity, often remaining immobile for weeks at a time. Sites where ambush behaviour was observed were frequently in close proximity (< 1 m) to game trails created by antelope, and new *B. gabonica* feeding records from my field work (e.g., Red Duiker; *Cephalophus*

natalensis) indicate individuals may target large prey (close to their own body mass) when available. The unique morphological adaptations of *B. gabonica* are discussed in the context of foraging ecology.

Ecological research from this study, coupled with new molecular data that shows South African and central African *B. gabonica* are genetically similar, suggests the South African *B. gabonica* population's conservation status is better than what was previously assumed. However, long-term protection and management of the coastal dune forest corridor (found primarily inside the iSimangaliso Wetland Park) is needed for a viable, local *B. gabonica* population. A handbook is provided specifically for Park staff which summarizes the ecology and threats to *B. gabonica*, and provides up-to-date management decisions on controversial protective measures (e.g. translsocation).

DECLARATION

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



Jonathan K. Warner January, 2009

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Chapter 1: Introduction

1.1 Snake research in southern Africa

Worldwide, reptiles are often neglected in research endeavours, planned management initiatives, and conservation efforts. Southern Africa is no exception in this respect. Despite high levels of reptilian diversity (currently more than 500 described species) and endemism (78%) in Southern Africa, the latest Red Data Book for the group (Branch 1988) is outdated in comparison to those of other taxa such as the mammals, amphibians and vascular plants (see Friedman & Daly 2004; Minter et al. 2004; Golding 2002) and in overall relevancy due to recent research and new, internationally recognized IUCN red-listing criteria (see IUCN 2001; 2003). Nonetheless, the future of reptilian studies in the region is exciting. Primarily as a response to deficient distribution data for many species of reptile, the Southern Africa Reptile Conservation Assessment (SARCA; the reptile equivalent to the The Southern African Frog Atlas Project; see Minter et al. 2004) was recently launched and is due to be published in 2009. Other noteworthy herpetological endeavours in Southern Africa currently focus on phylogenetics and the establishment of an alpha-level taxonomy for reptiles of the region (Branch et al. 2006).

While the resolution of distributional and taxonomical issues is laudable and necessary, fruitful conservation practices must also be informed by species-specific ecological data, information which currently does not exist at even baseline levels for the vast majority of reptile species in Southern Africa (Branch 1998). In the current technophilic world, the study of natural history and field biology appears increasingly irrelevant to many, even within the scientific community (Bury 2006). To the contrary, understanding how organisms interact with their environment is critically important to conservation efforts, especially as the globe becomes increasingly transformed by a burgeoning human population and human-dominated landscapes. Until Planet Earth is rendered anaemic enough to warrant “the naturalist” obsolete, field ecological studies must continue to be a key component of the multidisciplinary approach that is needed to understand and protect the complex natural world of which mankind is very much a part.

Recent reviews and data collected from tropical African reptiles – snakes in particular – have helped advance community ecology theory (Luiselli 2007), understanding of resource partitioning and rarity

(Luiselli 2006a) and reptile interpopulation dynamics (Luiselli 2006b). However, museum and lab-based research on ophidians has steadily increased (see Shine et al. 1998; Keogh et al. 2000; Shine et al. 2006a; Shine et al. 2006b), while field studies of free-ranging African snakes remain relatively depauperate (but see Alexander 2007); most glaringly in Southern Africa where reptile diversity is the richest in the continent.

Explanations for the scarcity of field research and consequent lack of knowledge regarding African snake species are varied and somewhat justifiable. Snakes are among the most maligned and misunderstood animals in the world; the fear that many people harbor towards snakes is perhaps nowhere more discernable than in Africa, where rural lifestyles, cultural superstitions, and medically important species often intermix. Although Africa has approximately 400 species of snakes, many are cryptic or have very elusive habits (i.e. the diverse fossorial genera) and over 90 are venomous (some highly so); making observation and handling of wild snakes difficult (Luiselli et al. 1998). Field studies are also hampered by strong logistical constraints like expensive and inaccessible field equipment, difficulty and danger associated with working in remote locations, and continuing trends of political instability in many African nations (Angelici et al. 2000). Basic biological data for most snake species on the continent are therefore largely unknown; rendering conservation management of snake taxa presumptuous at best, or in many cases, absent altogether. This is worrisome, given that the viability of some species requires specialized protection of particular habitats or other resources (Dodd 1987; Reinert 1992a; Dodd 1993), and because snakes play important ecological roles in many different ecosystems (Greene 1997; Alexander and Marais 2007; Luiselli 2006b)

1.2 Study animal

1.2.1 Biology

The focal animal of my research was the Gaboon Adder (or Gaboon Viper) *Bitis gabonica*, one of Africa's most recognizable snakes. A sedentary species renowned for its striking geometric patterning, the world's heaviest viper is nonetheless notoriously cryptic in its natural environment. Stocky and often obese in appearance, the species can attain lengths up to 2 m, although South African individuals rarely exceed 1.3 m (Bodbijl 1994). The disproportionately large head of *B. gabonica* resembles a dead leaf, complete with a dark dorsal stripe that mimics a midvein. Among snakes, Gaboon Adders have the longest fangs (max. 40 mm) and highest venom yields: Marsh and

Whaler (1984) report a max. wet yield of 9.7 ml, with injection quantity strongly correlated to snake body mass. Bites from *B. gabonica* are medical emergencies (Branch 1998) but the species is of docile disposition and the majority of bites occur from handling of captive individuals by snake enthusiasts (Wildi et al. 2001). Envenomation incurs mostly cytotoxic symptoms, although toxic effects to humans are not well known (Mallow 2003), and only one human death is described in the literature (Marsh et al. 2007). Thirty-five proteins (mostly serine proteinases) belonging to 12 toxin families have been identified in *B. gabonica* venom (Calvete et al. 2007).

Combat occurs between male *B. gabonica* during the mating season, with dominant males mating with females (Akester 1979). Like most species in the Viperidae, the species is viviparous. *Bitis gabonica* produce 16-43 offspring, presumably biennially or triennially (Bodbijl 1994; Branch 1998), but breeding cycles are understudied and probably variable at the population level. There are two known instances of hybridization between *B. gabonica* and *B. arietans* in the wild (Broadley and Parker 1976; Broadley et al. 2003), and one record of hybridization with *Bitis nasicornis* (Hughes 1968). *Bitis gabonica* is an ambush predator that feeds primarily on small mammals (Luiselli and Akani 2003; Perrin and Bodbijl 2001a). Several authors (Luiselli 2006; Perrin and Bodbijl 2001b) have speculated that the species is locally responsible for high levels of rodent depletion. Throughout sub-Saharan Africa, Gaboon Adders are associated with tropical and subtropical forests, although adjacent environments (i.e. savanna, woodland) are used to varying degrees among individuals (this study; Linn et al. 2006; Angelici et al. 2000). *Bitis gabonica* can be broadly classified as having crepuscular and nocturnal movement and feeding habits, but this is also individually variable and may differ seasonally and according to mating patterns (see Chapter 3).

1.2.2 Distribution

Core distribution is Central African, from Benin (where the species is a delicacy eaten in soups; Pitman 1938) to southern Sudan in the north, southwards to northern Angola and Zambia (Fig. 1). Moderate to small isolated populations exist in Tanzania, Malawi, Mozambique, Zimbabwe, and South Africa (Spawls & Branch 1995; Bodbijl 1994).

The distribution of *B. gabonica* in South Africa was not accurately known until this study, as many historical records have poor spatial resolutions (i.e. QDS; see Bourquin 2004) that are not adequate for high resolution habitat correlation purposes. Within South Africa, Gaboon Adders are restricted

to the subtropical forests of northeastern KwaZulu-Natal. Most of this habitat in South Africa exists as a narrow (100 m to several kms wide), linear stretch of coastal dune forest at the eastern extremity of the Mozambique coastal plain. Records exist from as far south as Umtunzini (28º57'S, 31º44'E) and inland as far as Manguzi (26º59'S, 32º45'E) and Matubatuba (28º25'S, 32º12'E) (Armstrong 2001, Bodbijl 1994). The range extends north into southern Mozambique (Manhica is the most northern record) but there is currently a large disjunction (~ 450 km) between records in extreme southern Mozambique and records in northern Mozambique and eastern Zimbabwe. The gap in the distribution in central Mozambique is a true disjunction and not simply due to a lack of data (W. Branch, pers. comm.), but *B. gabonica* range is probably more extensive in Mozambique than currently interpreted by distribution maps.



Figure 1.1 Distribution of *B. rhinoceros* and *B. gabonica* in Africa (adapted from Spawls and Branch 1995). A = The "Dahomey Gap;" a mosaic of dry forest and savanna that separates the Upper and Lower Guinean Forests. Sympatric *B. rhinoceros* and *B. gabonica* populations are presumed but not verified in this region (Mallow et al. 2003). B = The southernmost *B. gabonica* population; focal subject of this study.

1.2.3 Taxonomy

Two distinct subspecies have been recognized for a considerable time (see Mertens 1951), the Central African Gaboon Adder (*Bitis gabonica gabonica*) and the West African Gaboon Adder (*Bitis gabonica rhinoceros*). The West African Gaboon Adder occurs from Togo westward to Guinea (Fig. 1) and is characterized by large nasal horns and one dark eye-stripe (the Central African type has two distinct stripes running from the eye to the labial scales; Branch 1998). The molecular studies of Lenk et al. (1999) suggested that the two subspecies should be raised to specific status (*Bitis rhinoceros* and *Bitis gabonica*); this recommendation is followed here, and has been adopted by other researchers (e.g. Penner et al. 2008).

1.2.4 South African perspective

One of many species of conservation concern in South Africa, the Gaboon Adder (in South Africa known also as *umanqunjwana* [isiZulu] and *Gaboen adder* [Afrikaans]) is dependent on management practices based on sound ecological understanding for long-term sustainability. Although not listed in the 2000 IUCN Red List of Threatened Species (Hilton-Taylor 2004) that assesses global status, *B. gabonica* is red-listed in South Africa as "Vulnerable" (Branch 1988) and is provincially protected in KwaZulu-Natal (Ordinance 15 of 1974). *Bitis gabonica* occurs in the forest ecoregion in South Africa, one of the smallest biomes in the country and home to a variety of species regionally under threat from strip-mining, land invasion and land transformation by humans (Mucina and Rutherford 2006). Historically, much forested habitat in the country was destroyed for the cultivation of sugarcane and *Pinus* and *Eucalyptus* plantations (Lawes 2002; Armstrong 2002). Although widespread in other parts of Africa, the species distribution is very restricted in South Africa and is mainly contained by the iSimangaliso Wetland Park (henceforth iSimangaliso; formerly the Greater St. Lucia Wetland Park).

Rising rural population densities in South Africa have increased pressure on indigenous wood resources; nowhere is this more evident than the Dukuduku and Manguzi lowland forests in KwaZulu-Natal. Within the coastal plain, the 2500 ha Dukuduku Forest was generally regarded as harboring the densest population of *B. gabonica* (Kyle 2002; Bodbijl 1994). This is no longer true for the species, as the area has been systematically deforested due to slash and burn agriculture, and tree-felling for fuel and living structures by thousands of impoverished settlers (Lawes et al. 2004). Similarly, the once expansive Manguzi Forest has dwindled from ~5,600 ha to an isolated remnant of

489 ha (Kyle 2004), and although the species historically occupied this area, the present status of *B. gabonica* in Manguzi is unknown (R. Kyle pers. comm.) and has possibly been extirpated here. In addition to habitat destruction, illegal collection for the pet trade, road mortality, indiscriminate killing, *umuthi* (traditional medicine) and unsuitable/unnatural fire regimes also threaten *B. gabonica* in South Africa.

A representative member of a unique and uncommon coastal ecosystem for millennia, 'suitable habitat' in South Africa for *B. gabonica* has never been adequately defined. Bodbijl (1994) conducted the first radiotelemetric study on *B. gabonica* in the Dukuduku Forest, a study which included an important dietary analysis for Gaboon Adders in Dukuduku Forest (Perrin and Bodbijl 2001a). However, Bodbijl's (1994) work was hindered by a small sample size and lacked in-depth spatial and quantitative habitat analyses; critical ecological information for conservation management. Additionally, increasing human activities all but guarantee the imminent elimination of *B. gabonica* in unprotected areas, most importantly, the Dukuduku Forest, where Bodbijl's research was conducted. My research therefore focused on gathering data from *B. gabonica* in the protected iSimangaliso area; the last stronghold for the species in South Africa.

Because *Bitis gabonica* is locally threatened and faces conservation challenges similar to other species in the greater iSimangaliso area, Ezemvelo KwaZulu-Natal Wildlife (EKZNW), a co-manager of iSimangaliso, has agreed to "facilitate and support management-related research" on the species (EKZNW 2004). Under this context, I set out to study the ecology, life-history and conservation biology of *B. gabonica* in South Africa. My research was hosted by the iSimangaliso Threatened Species Project, a joint initiative of EKZNW and the iSimangaliso Wetland Park Authority. This Project aims to update distributional and biological data of rare, threatened and endemic species within iSimangaliso by facilitating research and conducting long-term studies on lesser-known flora and fauna often overlooked in favour of more charismatic species.

1.3 Research approach

Chapter Two of this dissertation describes the study site where I radiotracked *B. gabonica* in iSimangaliso. Also included is a discussion of methodology surrounding radiotelemetry, the primary tool used to gather ecological data from free-ranging *B. gabonica*.

Chapter Three focuses on the spatial ecology of radio-tracked *B. gabonica*. Specifically, the home ranges, seasonal movement patterns and behaviours associated with movement are discussed. Home ranges are interpreted using minimum convex polygons (MCPs) and isopleth kernel density (KD) estimates (Worton 1989). KD estimates are useful delineators of seasonal ranges and core areas (50% isopleths) of movement. The incorporation of KDs in my analysis is the first use of the method for an African snake species.

Habitat selection by *B. gabonica* is the focus of Chapter Four. A hierarchical approach is employed to clarify the intertwined importance of macro- and microhabitat to the species. Using a suite of habitat variables collected from where snakes were located, and at random sites, I tested for differences among habitat characteristics for three variables: season, sex and habitat selection. The influential habitat variables contributing to differences among types of sites were analyzed and discussed. Updated distribution maps of *B. gabonica* distribution in South Africa are presented as inferred from habitat availability and historical records.

Chapter Five investigates the foraging ecology and diet of *B. gabonica*. Hunting behaviour, prey choice and ecdysis are discussed in terms of habitat selection, movement and feeding success. New feeding records are presented for the species, and a comprehensive list of recorded prey is presented for *B. gabonica* across its range. Selection pressures related to feeding and influencing *B. gabonica* morphology are also discussed.

The final chapter is a concluding chapter that highlights the results of my study. Conservation implications of research findings are discussed, specifically genetic similarities between *B. gabonica* populations, and the importance of iSimangaliso to the future viability of South African *B. gabonica*. Suggestions for future *B. gabonica* research are presented.

An addendum is included that addresses the interface between *B. gabonica* ecology and practical conservation of the species in South Africa. This section is a summarization of the ecological findings of my study and is presented in a handbook format for Park managers and staff. Management implications and controversial issues such as translocation and proper burning regimes are discussed in a context appropriate to recent management decisions regarding *B. gabonica* in the greater Park area.

Chapter 2: Description of study site and radiotelemetry methodology

2.1 Study site

I conducted my research on *B. gabonica* from 2005 to 2007 in the iSimangaliso Wetland Park (iSimangaliso). This park lies on the south-eastern coast of Africa in the province of KwaZulu-Natal in the Republic of South Africa (Fig. 2). Originally proclaimed as "St Lucia Reserve No. 1" in 1895, iSimangaliso is among the oldest extant reserves on the continent and currently consists of thirteen contiguous protected areas totalling 239,566 ha (KZNNCS 1998). In 1999 iSimangaliso was declared a UNESCO World Heritage Site.

Formed during the break up of Gondwanaland 140 million years ago, the Lebombo Mountain Range represents the continental rift line and borders iSimangaliso to the west (Goodman 1990). The majority of the Park is found on the tapering southern extremity of the Mozambique (East African) coastal plain, a feature formed by deposits of sediment over a base of igneous rock during the Cretaceous period by terrestrial and marine sedimentary material of the Zululand Group (Maud 1990). As sea levels retreated and advanced with global glacial fluxes throughout the Tertiary and Quaternary, the coastal plain was repeatedly exposed and submerged as it underwent cycles of sedimentation and erosion by marine and aeolian processes. Today, the majority of the coastal plain consists of young, infertile sands. Current and interrelated fluvial, marine and aeolian processes were initiated in the Pleistocene and are responsible for the various pans, swamps, saline and freshwater lakes, estuaries and beaches that presently make up the greater iSimangaliso area. The vegetation of the region occurs in a diverse mosaic of forests, thickets, woodlands, grasslands, and wetlands. Wind-driven sands are responsible for the formation of the region's most predominant feature; a series of bi-directional, parabolic dunes that run parallel to the coastline (Goodman 1990). These vegetated dunes span 280 km of protected coastline and are among the tallest in the world, reaching a maximum height of 183 m (van Wyk 1994).



Figure 2.1 Map of the Maputaland Centre of Endemism (MCE) and the iSimangaliso Wetland Park (iSWP). Adapted from www.mosaic-conservation.org

iSimangaliso has a subtropical climate with warm, moist summers and mild winters. The Indian Ocean's Agulhas current generates a notable warming influence on the area and the mean annual temperature for the region exceeds 21 ^{o}C. Temporally and spatially, rainfall is highly variable, with

an overall climatic gradient of high rainfall (1200-1300 mm/year) and evaporation (1300 mm/yr.) in the eastern coastal zone to drier conditions (rainfall <600 mm/yr.; evaporation 1660 mm/yr.) inland to the west (Watkeys et al. 1993). Sixty-percent of the rainfall occurs in summer (Southern Hemisphere; November to March) and episodic large-scale floods occur due to tropical cyclones. Despite relatively high evaporation levels, the area is humid year-round. Prevailing regional winds are north-easterly and south-westerly (KZNNCS 1998).

iSimangaliso is an area of extraordinary species richness and home to many species that are of conservation concern. Herpetofaunal diversity of the area underscores this, with approximately 160 species. Sixteen species of reptiles that occur within the park's boundaries are listed in CITES appendices (Schedule 14), five species of frogs are endemic to KwaZulu-Natal, and several species of reptiles (*Prosymna janii*, *Scelotes vestigifer, S. fitzsimonsi, Bradypodion setaroi*) are exclusive to the coastal dune system that is largely contained within the park (Broadley 1990; KZNNCS 1998). iSimangaliso is the largest protected area in Conservation International's Maputaland-Pondoland-Albany hotspot (Smith 2001). The Park also forms part of the Maputaland Centre of Endemism (Smith 2001), a 20,000 km^2 region between the Limpopo and St. Lucia estuaries, and consists of the Lebombo Mountain range and coastal plain (Fig. 2.1). The latter is the southern extremity of the East African coastal plain; consequently many species reach their southernmost limit in Maputaland. In addition to being an area of integration between tropical and subtropical biota (Bruton and Cooper 1980), Maputaland also harbours numerous endemic species of flora and fauna, probably as the result of *in situ* speciation on the geologically recent coastal plain. Well-defined climatic and geological gradients are responsible for the distinctive ecological zones of the region, which further contribute to high gamma diversity in north-eastern KwaZulu-Natal (Smith 2006).

The majority (91%) of telemetred *B. gabonica* in my study were tracked on the "Eastern Shores" section of the Park; a 12873 ha area located between Lake St. Lucia and the Indian Ocean. The Eastern Shores contains hydromorphic and dry grassland areas, closed and open woodlands, and swamp and coastal dune forest vegetation types (KZNNCS 1998; Mucina and Rutherford 2006). Due to former *Pinus* and *Eucalyptus* plantations (5000 ha), secondary grassland and forest are also present in this region. Although other habitats are utilized, the coastal dune forest macrohabitat is of primary importance for *B. gabonica* (see Chapter 4).

2.2 Radiotelemetry methodology

2.2.1 Introduction

Varied technological advancements and broadening taxonomic views regarding conservation and research pertaining to "non-game" organisms have allowed for a marked increase in the number of field-based reptile studies over the past two decades (Shine & Bonnet 2000). Heightened interest in snake biology among research programmes and the parallel miniaturization of radiotransmitters have revolutionized the study of snake ecology through radiotelemetry. Since the pioneering efforts of Fitch (1971) and Reinert (1984a; 1984b; Reinert and Kodrich 1982), many notable telemetry projects on snakes have been undertaken worldwide, including many on viperids (for examples see Diffendorfer et al. 2005; Pearson et al. 2003; Weatherhead & Charland 1985; Shine et al. 2003; Whitaker & Shine 2003; King et al. 2004; Moore & Gillingham 2006; Marshall et al. 2006; Rodriguez-Robles 2003).

Nowadays, some radiotransmitter models are small enough to be clipped to the wings of insects and others powerful enough to be detected by satellites (Cooke et al. 2004). The development and popularity of biotelemetry stems from the unparalleled glimpse the technology provides into the activity patterns of animals through discriminatory monitoring, or "tracking." Cryptic taxa such as snake species are ideal candidates for radiotelemetry and are gaining in research popularity because they now make for accessible ecological models (Shine and Bonnet 2000). Monitoring wild snakes with radiotelemetry allows researchers in-depth observations of snake movement and habitat use patterns that can be used to assist conservation and species-protection purposes (Reinert and Zappalorti 1988).

2.2.2 Surgical procedures

I radiotracked eleven *B. gabonica* between December 2005 and April 2007 (Table 2.1). Due to the species' cryptic nature and its presumed rarity, I initially searched for *B. gabonica* using a trained male German Shorthaired Pointer dog. After experiencing limited success with this method, I acquired *B. gabonica* by collecting specimens located at park campsites and staff quarters and those located during bush-clearing operations, road-cruises, and opportunistically while conducting

radiotelemetry field work. I also distributed a flyer in English and isiZulu encouraging iSimangaliso managers to report and capture any *B. gabonica* observed by staff in their respective sections.

Table 2.1 Critical data for telemetered *B. gabonica*

Snake No.	Relocated	Sex	Stage	SVL (mm)	Tail (mm)	Body Mass (g)	Period Tracked DD/MM/YY	Days Tracked	Mortality
1	N	♂	Ad	984	105	980	05/12/05-23/04/07	504	N
2	Y	♀	Ad	1210	92	1864	06/12/05-21/09/06	289	Y[1]
3	N	♂	Ad	887	102	1288	15/03/06-11/07/06	114	N
4	Y	♂	Ad	1000	130	1934	10/04/06-12/01/07	277	N
5	Y	♂	Ad	975	120	1422	17/04/06-15/03/07	332	N
6	N	♀	Ad	899	60	1242	19/04/06-13/03/07	328	N
7	Y	♂	Ad	1050	126	1390	01/08/06-15/12/06	136	N
8	Y	♀	Ad	1164	77	3900	09/11/06-07/03/07	177	N
9	N	♀	Ad	750	40	918	10/11/06-23/04/07	164	N
10	N	♂	Juv	310	35	101	24/12/06-06/01/07	13	Y[2]
11	N	♂	Ad	934	121	1350	28/03/07-25/04/07	28	N

[1]Cause unknown, [2]Predated

I implanted transmitters into seven male and four female *B. gabonica*. Transmitters were either 35.0 g (avg., sealed in wax; Vutech Heat Transmitters, South Africa), or 13.0 g or 5.0 g transmitters (Models SI-2 and SB-2; Holohil Systems, Ltd., Ontario, Canada). All transmitters operated within the 149-150 MHz frequency range. Transmitter mass was 5.5% (± 0.1%) of snake body mass for two individuals and under 3.5% for all others. All surgeries were conducted at the EKZNW research lab in St. Lucia. Snakes were anteriorly restrained in a polycarbonate tube and then anesthetized with ketamine (Ketaset, 100 mg/kg) by intramuscular injection on the dorsal surface above the point of incision. Individuals also received small dosages of lignocaine (Xylocaine, ≤ 1 mg), a local anaesthetic. Each individual was measured (SVL, tail length), weighed, and placed back in cages

until a suitable level of anaesthesia (unresponsiveness) was obtained (approximately 40 minutes). Surgical procedures were adapted from Reinert and Cundall (1982), with the incision made in the posterior third of the snake between the first and second dorsal scale rows (Figure 2.2). Transmitters were inserted in the peritoneal cavity. The antenna was either inserted with the transmitter or positioned subcutaneously. Post-surgery, snakes were injected with enrofloxacin (Baytril, 25 mg/kg) to minimize bacterial infection and were kept in clean cages until release 5-10 days later. No mortalities were attributed to surgical procedures, although one *B. gabonica* was removed from the study upon acute infection of the incision area.



Figure 2.2 Lateral incision for transmitter insertion

2.2.3 Fieldwork

When feasible, I released telemetered Gaboon Adders at their points of capture. However five of the eleven (45%) snakes were relocated to new areas within iSimangaliso, in comparable habitats of known *B. gabonica* occurrence (based on historical records). Only one individual (adult ♀) was translocated from outside the greater iSimangaliso area (Umtunzini). The value of translocation as a conservation management tool is a controversial but requisite topic, as it may be beneficial for some

Table 2.2 Data variables collected at each *B. gabonica* radiolocation

Variable	Description	Example Entry
Snake ID	Snake being tracked	1♂
Entry Number	Represents how many times a snake has been tracked	25
Site Number	New for each movement event >5 metres	17
Telemetry Check	Yes/No	Yes
Visual	Yes/No	Yes
Tracker	Person tracking snake	JKW
Observer	Person(s) accompanying tracker	XC, SS
Date	Date of fix	17-Apr-06
Time	Time of fix	13:22
General Location	ES (Eastern Shores) or WS (Western Shores)	ES
Common Location	Position of snake relative to previous fix	10m NE
Macrohabitat	Dune Forest (DF), Swamp Forest (SF), Woodland (WD), etc.	DF
GPS	Location of snake as saved in GPS unit	M10417
Precipitation	NR (no rain), SP (sprinkle), LR (light rain), MR (moderate rain), or HR (heavy rain)	NR
Cloud Cover	0 (clear), 1, 2, 3, or 4 (100% cover)	3
SAT	Shaded air temperature (°C), recorded 1m above snake	26.5
HUM	Humidity (%), recorded on ground 1m from snake	75
SUB	Substrate temperature, recorded 1m from snake	17.5
Wind	Wind speed (m/s, avg. for 30 seconds), recorded 1m above snake	0.3
Action	Is snake lying still (LS) or moving (MV)	LS
Body Position	Is snake coiled (CL), "S"-curved (SC), looped (LP), or straightened out (SO)	SC
Sun Exposure	Is snake in full sun (FS), full shade (FD), or partial/dappled sun (PS)	PS
Visibility	Is snake fully exposed (FX), partially obscured (PC), or completely covered (CC)	PC
Notes	Short summary of snake behaviour/condition	Basking at thicket edge in *Isoglossa woodi*

threatened species (Dodd and Seigel 1991; King et al. 2004). While relocation of wild individuals was not initially intended for this project, it became a necessary course of action due to 1.) Inadequate numbers of telemetered individuals that could be released at their capture localities and 2.) Current EKZNW policy of releasing *B. gabonica* captured outside the protected area (e.g. St. Lucia village, Dukuduku Forest) into iSimangaliso. Radiomonitoring of translocated *B. gabonica* therefore dovetailed with current conservation activities for the species and provided insight into the viability of translocation as a future management practice.

I tracked each telemetered snake three to four times per week when possible (adequate for sedentary species; Reinert 1992). Effort was made to obtain radiolocations (fixes) for each individual at alternating periods of the day (morning, afternoon, evening). In several instances, I had to abort tracking efforts due to *B. gabonica* locations in close proximity to potentially dangerous game; namely Buffalo (*Syncerus caffer*), Rhino (*Ceratotherium simum*), Elephant (*Loxodonta africana*), Hippo (*Hippopotamus amphibious*), and Crocodile (*Crocodylus niloticus*). Night fixes were discouraged by Park management so nocturnal data were not collected.

At each radiolocation, I recorded locational, environmental, and behavioural data (Table 2.2). Although telemetred snakes rarely showed distress (hissed or moved) due to my presence, time spent at each fix was usually restricted to less than five minutes to minimize disturbance. Fix locations were recorded with a Garmin© GPS 12XL. Because of GPS positional error, and inaccuracies with interpreting minor "adjustment" movements for home-range and seasonal spatial analyses (see Chapter 3), a new location was designated only when a snake had moved a linear distance of 5 m or greater from the previous site. When visual observations were not possible I obtained fixes using triangulation. Environmental variables were measured using a Kestrel 3000 Pocket Weather Meter and a Reo*Temp* Bimetal Thermometer. Lastly, each site was marked with vinyl flagging tape for microhabitat analysis subsequent to the snake moving out of the area (Chapter 4).

Chapter 3: Spatial ecology

3.1 Introduction to snake spatial ecology

Most published research suggests that movement by snakes is highly deterministic, and that movement events and activity patterns are the result of stimuli, both of extrinsic and intrinsic origins (Gibbons and Semlitsch 1987). However, the casual processes that cause movement (disturbance, breeding instincts, etc.) are copious, often abstruse, and usually difficult for researchers to observe. Historically, therefore, the principal aim of many activity studies on free-ranging animals has been to generate descriptive spatial data (i.e. home range areas, movement distances). However, knowledge of a species' spatial ecology must be bolstered not only by descriptive data, but also with a commensurate interpretation of causation of movement, from individual events to species-wide activity patterns, within the context of ecological and evolutionary significance (Gregory et al. 1987; Whitaker and Shine 2003). Understanding the relationship between observed activity patterns and casual influences is important not only for a competent awareness of snake biology, but also for conservation purposes—understanding activity patterns and correctly interpreting why reptiles move when they do can lead to improved management practices and better protection of habitat (Bonnet et al. 1999).

Radiotelemetry has considerably aided research endeavours to combine both descriptive and interpretative movement approaches to achieve a more complete understanding of activity for many snake species. Recent studies have relied increasingly on radiotelemetry monitoring to expose the importance of reproductive condition (Reinert and Kodrich 1982), thermoregulatory requirements (Shine et al. 2003), foraging strategies (Reinert et al. 1984), disturbance (Parent and Weatherhead 2000), shifts due to ambient weather conditions (Pearson et al. 2003) and social interactions (Reinert 1984) in defining the activity patterns of snakes from various taxa.

The spatial ecologies of tropical and subtropical snakes are largely unknown in comparison with temperate species (Greene 1997; Branch 1998). Consequently, contemporary understanding of snake activity patterns often operates within a "Temperate, Northern Hemisphere" paradigm to explain

ecological similarities observed across taxa. The cornerstone of this paradigm is that species use hibernacula in winter and therefore show strong seasonality in terms of movement. With the possible exception of some extreme southerly races in high altitudes, African squamates do not brumate. Thus, it remains to be seen for most species how strongly seasonal influences affect movement patterns.

Although basic biological information is lacking for many African snakes (Alexander and Marais 2007), *Bitis gabonica* has received much research attention in recent years, and this study is the fourth that uses radiotelemetry to gain insight into the spatial ecology of this wide-ranging species (see Angelici 2000; Lawson 2006; Linn et al. 2006). Previous monitoring attempts have demonstrated that across the distribution individual *B. gabonica* are largely sedentary, although variation in home range size is observed in all published spatial data on the species (Table 3.1). Understanding of the frequency, conditions, and seasonality of *B. gabonica* movement has remained deficient, partly because pioneering radiotelemetry research on the species was limited by small sample sizes (Table 3.1). It should also be noted that previous studies are biased towards tropical areas (Cameroon: Lawson 2006, Nigeria: Angelici 2000).

Table 3.1 Home ranges (MCPs) of *B. gabonica* from three previous radiotelemetry studies in Africa (*relocated snake)

Study	# Days tracked	Sex	Home range (ha)
Angelici et al. 2000	20	♂	1.60
Angelici et al. 2000	20	♀	0.80
Linn et al. 2006	361	♂*	576.60
Linn et al. 2006	225	♀	12.60
Linn et al. 2006	258	♀*	37.00
Lawson 2006	200	♀	38.29
Lawson 2006	65	♀	1.38

Here, building on previous research on the species, I present data and analysis on the spatial ecology of *B. gabonica* in South Africa gathered using radiotelemetry and field observations from ten snakes (six males and four females; an additional telemetered neonate was excluded from spatial analyses because data was only collected on movement for two weeks before the individual was predated) tracked in the iSimangaliso Wetland Park (iSimangaliso) between 2005 and 2007 (detailed radiotelemetry methodology is provided in Chapter 2). My purpose was to clarify the movement and activity patterns for the species at the southern extent of its range. I hypothesized that seasonal variation within the subtropical climate of northeastern South Africa is responsible for seasonal patterns of activity that could be observed through radiotelemetry monitoring. However, any patterns within the spatial ecology of *B. gabonica* were expected to be less pronounced when compared with temperate snakes that brumate annually.

I took a three-layered approach in examining movement activity for *B. gabonica*: First, I analyzed space-use at the broadest level, using several different estimators in calculating home range areas for telemetred snakes. Next, I considered the specific movement events that form home ranges, emphasizing shared seasonal patterns observed among *B. gabonica*. Lastly, I examined movement within a behavioural context, focusing on activity dynamics among individuals and movement behaviour common to *B. gabonica* in South Africa. Additionally, I dissected the causative factors and ecological consequences of the activity patterns and movement behaviour observed in an attempt to present a more comprehensive understanding of the spatial ecology of this unusual African snake.

3.2 Methods

3.2.1 Home range estimation

Within spatial ecology studies, an animal's "home range" is subject to a variety of titles and interpretations by researchers, and the concept itself is seen as contentious by some and rejected outright by others (Powell 2000). I took a mainstream approach with my usage and definition of home range, and simply used the term as a convenient label to represent the area used by individuals over a specified period of time; the defined space within which an individual lives. This definition does not assume nor refute "homing" ability by the snakes, and is theoretically congruous with

similar published snake spatial ecology studies. I used the Home Range Tools extension for ArcGIS (Rodgers et al. 2005) of the ArcGIS 9.2 software program (Environmental Systems Research Institute, Inc.) to calculate all home-range estimates. Lat/Long points used for home range analyses came from GPS waypoints representing *B. gabonica* locations. Because of GPS positional error and to compensate for minor *B. gabonica* body adjustments, a new site was only designated once the telemetered snake had moved a minimum linear distance of 5 m from the previously recorded locality.

I constructed a 100% minimum convex polygon (MCP) for each telemetered snake. MCPs are the oldest and simplest method for calculating home ranges. Minimum convex polygons are polygonal areas with no concavities and are constructed by connecting the outermost locations. All other localities are enclosed within the polygon, with the total area of the polygon representing the animal's home range (Jennrich and Turner 1969). Although MCPs are crude estimates of space use with many inadequacies (see White and Garrott 1990), due to their ease of measurement, MCPs are frequently used in the literature and are included here for comparative purposes with other studies.

I also used a more realistic method to calculate home ranges; kernel densities (KDs). The KD method is a nonparametric statistical estimator of an animal's home range that incorporates the density of known locations (in this case, GPS points obtained from fix observations), giving more weight to high density areas, to construct a home range density (or probability) contour consisting of a compilation of "kernels." These kernels are regions around point locations that contain a given likelihood of animal presence (Worton 1989). Home range contours can be of any shape and are superior measures to MCPs because they allow for multiple centres of activity and are more accurate indicators of an animal's partitioning and utilization of space (Kernohan et al. 2001).

For each telemetered *B. gabonica*, I calculated the 95% density contour (the area where the snake was found 95% of the time) and the 50% density contour (the area within the total home range where use was most concentrated). The 50% KD, or core area, is referred to as the activity centre in other snake spatial ecology studies (e.g. Secor 1994; Marshall et al. 2006). Activity centres do not have to be singular isopleths and may appear as "islands" of high activity separated by rarely used areas.

Correctly establishing kernel widths in KD analysis is critical for accurate construction of home range areas. Too wide a kernel will overestimate space use, whereas a narrow kernel will underestimate home range. Kernel width is based on a smoothing parameter (*h*), which is determined by one of two automated methods. The reference method selects *h* based on assumptions of bivariate normality, while the more frequently used least-squares cross validation (LSCV) method determines kernel width based on properties of the data (Kernohan et al. 2001). I used LSCV on my data to select *h*, as it is the best method for small data sets (applicable here because of the high level of inactivity by radiotracked *B. gabonica*, hence small numbers of independent locality points) and is also the only method used to select *h* in comparable published studies, thus standardizing my analysis.

Kernels can either be adaptive (*h* increases as the distance between kernels increases) or fixed (the *h* parameter is held constant throughout the analysis). Adaptive kernels are discouraged for movement studies because they over-estimate home range areas (Powell 2000; Kernohan et al. 2001); therefore I used the fixed kernel method. First, I determined individual *h* values using LSCV for each radiotracked *B. gabonica*, then found the mean *h* for all snakes. I then calculated KDs holding *h* constant for the locational dataset of each *B. gabonica* (fixed kernel). The fixed kernel estimator with LSCV produces the most accurate estimates of home range areas and is the best approach currently available (Seaman and Powell 1996; Powell 2000; Kernohan et al. 2001).

3.2.2 Activity and seasonal patterns

For each telemetred *B. gabonica*, I measured a suite of variables to assist in describing activity and seasonal patterns of space use. Movement measurements were rounded to the nearest meter. Frequency of movement was calculated by dividing the number of moves a snake made by the number of days it was tracked. Total distance moved was calculated by summing the linear distances between successive sites, and mean distance moved per day was found by dividing the total distance moved by the total number of days the snake was monitored. Finally, range length was calculated by measuring the linear distance between the two most distant sites a snake occupied in its home range. Nonparametric statistical tests were applied to these variables to check for differences between males and females, and resident and relocated *B. gabonica*.

I analyzed movement events to detect seasonal patterns, specifically looking at activity peaks. Statistical analysis of seasonal movements was preformed on data from five *B. gabonica* monitored for the entire winter (Southern hemisphere; June-August) and at least the months immediately preceding and following the winter season. I divided each month into two categories, using the 15th as the point of separation between the periods, resulting in 11 two-week periods (from the second half of April to the second half of September) for each of the five individuals (55 periods in total). I then calculated the distance moved by each snake during each period before running a Kruskal-Wallis test on the data using period as the grouping (or independent) variable, and distance moved as the dependent variable. This non-parametric test tests the null hypothesis that the different samples under comparison (in this case, distances moved by different snakes for each period) were drawn from the same distribution or from distributions with the same median. All statistical analyses were done using Statistica 6.0 with alpha levels (*p*-values) set at 0.05.

3.2.3 Observation of movement behaviour

Bitis gabonica is known to be crepuscular and nocturnal throughout its range. Because I could not conduct night fixes, it should be noted that sound conclusions about movement activity and behaviour are limited (for a good study that documents nocturnal activity of a tropical viperid using radiotelemetry, see Wasko and Sasa 2009). The infrequency of *B. gabonica* daytime movement events and scarcity of my field-observations of these events rendered quantitative analysis of movement behaviour (the activities involved with *B. gabonica* site relocation) impossible. However, I documented movement at several scales from *B. gabonica* fix observation data, focusing on body adjustments, body positioning, burrowing and general locomotory strategies.

3.3 Results

3.3.1 Multiple convex polygon and kernel density home range estimates

Multiple convex polygons estimates of home range for ten *B. gabonica* (six males, four females) averaged 28.58 ha (42.48 ha for males, 7.72 ha for females). For kernel density estimates, mean *h*

was 0.2129. 95% KD contour averages were similar in area to MCP averages (28.92 ha overall; 42.65 ha for males, 8.32 for females). Individual *B. gabonica* activity centres (50% KDs) ranged from 0.04-29.75 ha and averaged 6.74 ha, with the mean male activity centre almost 5 times greater than the mean female activity centre (Table 3.2).

Table 3.2 Minimum Convex Polygons and Kernel Densities for telemetered *B. gabonica* (* relocated snake)

Snake (days tracked)	Sex	Fixed Kernel		100% Minimum Convex Polygon (ha)
		Density Contour (%)	Area (ha)	
1	♂	95	47.20	43.23
(504)		50	12.82	
2*	♀	95	3.24	2.64
(289)		50	0.76	
3	♂	95	0.13	0.12
(114)		50	0.04	
4*	♂	95	62.02	60.80
(227)		50	13.08	
5*	♂	95	132.29	139.16
(332)		50	29.75	
6	♀	95	14.75	15.74
(328)		50	3.59	
7*	♂	95	2.19	2.00
(136)		50	0.47	
8*	♀	95	0.28	0.15
(177)		50	0.06	
9	♀	95	15.03	12.36
(164)		50	3.73	
10	♂	95	12.04	9.57
(28)		50	3.07	
Average	All	95	28.92 (41.92)	28.58 (43.80)
(SD)		50	6.74 (9.45)	
Average	♂	95	42.65 (50.62)	42.48 (53.29)
(SD)		50	9.87 (11.36)	
Average	♀	95	8.32 (7.68)	7.72 (7.50)
(SD)		50	2.04 (1.90)	

Shapiro-Wilk W tests for normality for MCP, 95% KD, and 50% KD estimator datasets determined the W statistic to be significant in all cases ($p < 0.05$, meaning the hypothesis that the data are normally distributed must be rejected). I applied the nonparametric Wald-Wolfowitz runs test to MCPs, 95% KDs, and 50% KDs to test for significant differences among males and females, and resident and relocated *B. gabonica*. This test is ideal for small datasets and the null hypothesis is that the two samples (i.e. male and female; resident and relocated home ranges) were drawn from the same population. Non-significant *p*-values (> 0.05) were calculated for each estimator for resident and relocated *B. gabonica* and for males and females. Although significant differences were not detected between groups, male home ranges tended to be larger than females (Fig. 3.1). Examples of "typical" *B. gabonica* male and female home range areas are presented in Fig. 3.2.

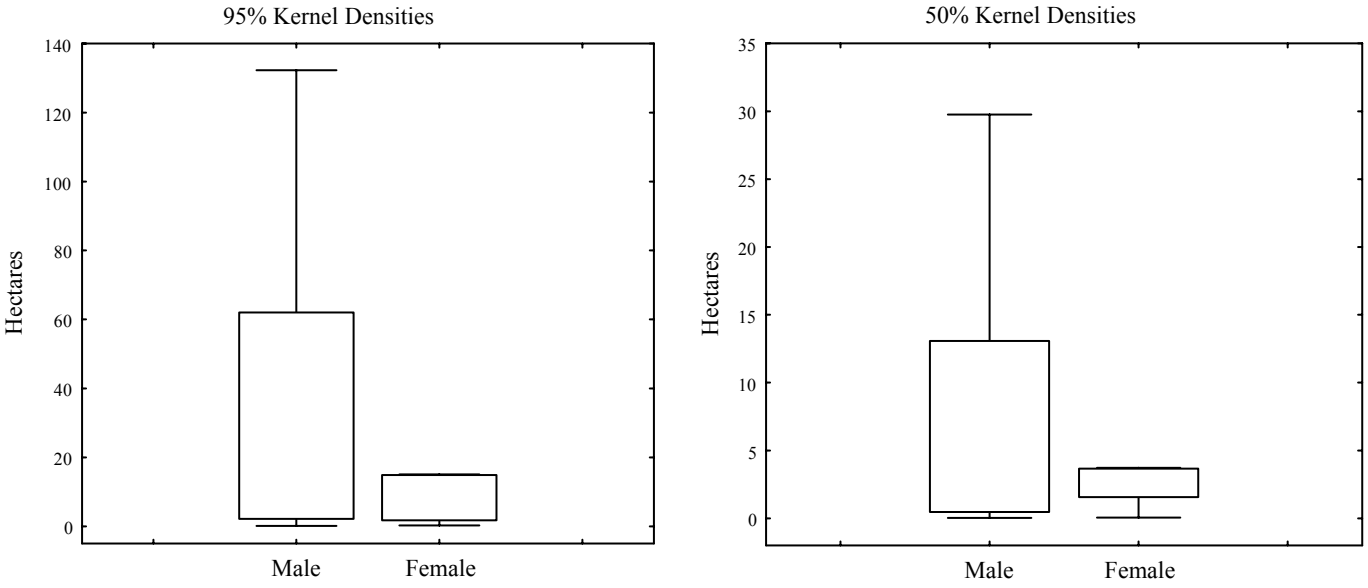


Figure 3.1 Kernel density descriptions for telemetered male and female *B. gabonica*. Boxes denote 25-75% percentiles, error bars denote min-max KDs.

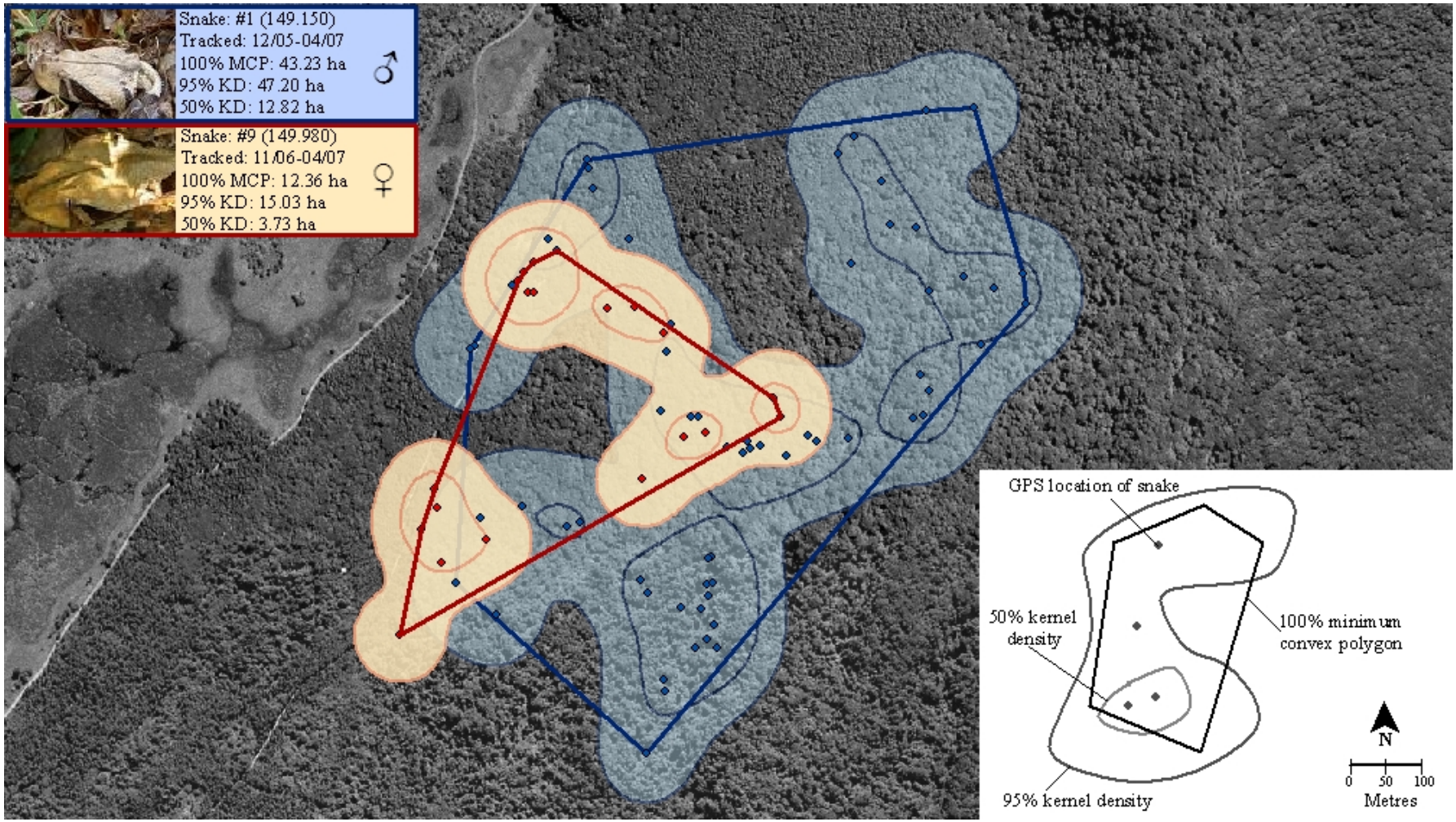


Figure 3.2 Representative home range estimates for male and female *B. gabonica*

3.3.2 Activity patterns

Telemetered *B. gabonica* were highly sedentary, as reflected both by average movement frequencies and total number of movements (Table 3.3). Typical movement behaviour during the activity season consisted of occasional small movements (< 15 m) within a particular area (although the time between these minor moves could be several days to several weeks), followed by a longer, continuous move (> 50 m). The largest single move by a tracked individual was 587 m (snake #5).

Table 3.3 Movement parameters for telemetered *B. gabonica*

Snake	Sex	Days tracked	Number of movements	Freq. of movement (% of days)	Total dist. moved (m)	Avg. dist./move (m)	Range length (m)
1	♂	504	61	12.10	3162	52	995
2*	♀	289	42	14.53	814	19	315
3	♂	114	12	9.50	162	14	83
4*	♂	227	28	10.53	2977	106	2744
5*	♂	332	42	12.65	4703	112	2536
6	♀	328	28	8.54	1807	65	648
7*	♂	136	12	8.82	528	44	319
8*	♀	177	5	2.82	133	27	93
9	♀	164	18	10.98	1165	65	604
10	♂	28	6	21.43	1222	204	601
All	Mean	229.90	25.40	11.19	1667.30	70.80	893.80
	(SD)	(136.96)	(8.37)	(4.77)	(1501.15)	(57.39)	(961.74)
Male	Mean	223.50	26.83	12.51	2125.67	88.67	1213.00
	(SD)	(172.24)	(21.32)	(4.61)	(1770.12)	(67.91)	(1148.26)
Female	Mean	239.50	23.25	9.22	979.75	44.00	415.00
	(SD)	(81.42)	(15.65)	(4.92)	(698.36)	(24.47)	(260.57)

Although male averages were larger than female averages in all movement categories, three non-parametric statistical tests (Kolmogorov-Smirnov, Wald-Wolfowitz runs, and Mann-Whitney U) detected no significant differences ($p > 0.05$) between male and female *B. gabonica* for any of the dependent variable categories listed in Table 3.3. Additionally, the same tests produced no significant differences between resident and relocated *B. gabonica*. Similar to home range averages for the two groups, averages for certain movement categories between resident and relocated snakes were close (Fig. 3.3). Relocated individuals did not differ in their movement trends to resident *B. gabonica*, and had similar variations in home range areas and specific movements.

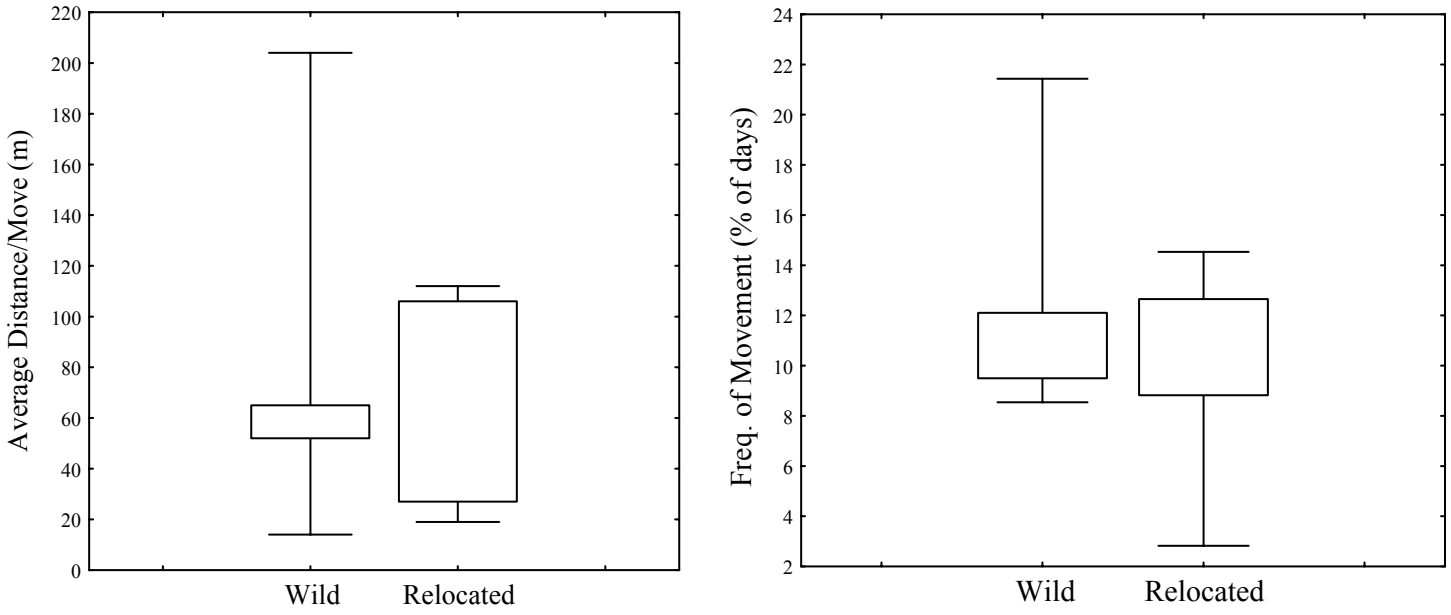


Figure 3.3 Movement distances and frequencies for telemetered resident and relocated *B. gabonica*. Boxes denote 25-75% percentiles; error bars denote min-max.

3.3.3 Seasonal movements

Although movement distances and home ranges were variable among individuals, a clear bimodal seasonal activity pattern was evident among telemetred *B. gabonica*, with movement peaks in the spring and fall. The fall activity peak was associated with the mating season, which occurs March-May in South Africa (Bodbijl 1994). During this time, *B. gabonica* are seen (and killed) crossing roads and found in residential gardens, and are more frequently observed by local inhabitants. In 2007, the mating season appeared to have started in early March; during a 24-hour period on March 11-12, three *B. gabonica* were reported (from reputable sources familiar with the species) crossing roads in the greater St. Lucia area, and one individual was captured in a guard camp at Mission Rocks (28° 16' 0.2", 32° 28' 52.5"). Five anecdotal but unverifiable *B. gabonica* sightings were also reported in early March. This timeframe closely coincided with the beginning of a period of increased movement among radiotracked snakes (males and females), with all individuals making at least one movement of over 150 metres during the month (Table 3.4). Two individuals (#5 and #8)

were permanently lost during this time (Table 3.4). Although other causes for the disappearance of these two snakes are possible (i.e. predation), it is highly likely that they moved out of radio contact given the predisposition for individuals to move much greater distances in autumn (although movement itself increases mortality risk for some species; Bonnet 1999). Telemetered *B. gabonica* did not brumate in the true sense, but did become extremely inactive during the winter months (Southern hemisphere; roughly June-August). During the winter period individuals remained immobile for months at a time, and in one notable case, a female (snake #6) did not move (except for very minor body adjustments) for 87 days (Table 3.5). Results of the Kruskal-Wallis test showed a significant difference between distance moved and time of year for five individuals tracked for the duration of the winter season ($p < 0.05$; Fig. 3.4). Winter inactive periods were also observed in all other telemetered snakes, but these individuals were excluded from the analysis because of incomplete seasonal monitoring.

Table 3.4 Movement data for telemetered *B. gabonica* during March 2007

Snake (sex)	Number of moves >50 m	Total distance moved (m)
1 (♂)	5	463
5 (♂)	3	>660 (lost)
6 (♀)	2	265
8 (♀)	1	>500 (lost)
9 (♀)	4	477
10 (♂)	6	1222

Table 3.5 Winter inactivity periods for telemetered *B. gabonica*

Snake (sex)	Inactive period (2006)	Days inactive	Total moves	Number of moves >50 m	Total dist. moved (m)
1 (♂)	6 Jul-11 Sep	64	2	0	55
2 (♀)	19 Jun-22 Jul	34	2	0	13
3 (♂)	3 Jun-11 Jul	38	3	0	37
4 (♂)	6 Jul-4 Sep	60	2	0	35
5 (♂)	6 Jul-12 Sep	69	0	0	0
6 (♀)	9 May-2 Aug	87	0	0	0
7 (♂)	1 Aug-4 Oct	65	2	0	23

A spring peak in activity among individuals followed the winter inactivity period and extended into the early summer. Several telemetered *B. gabonica* decreased movement activity as the hot summer months continued, resulting in moderate periods of inactivity for some snakes in late January and February (max. 38 days; snake #6) before the fall active season.

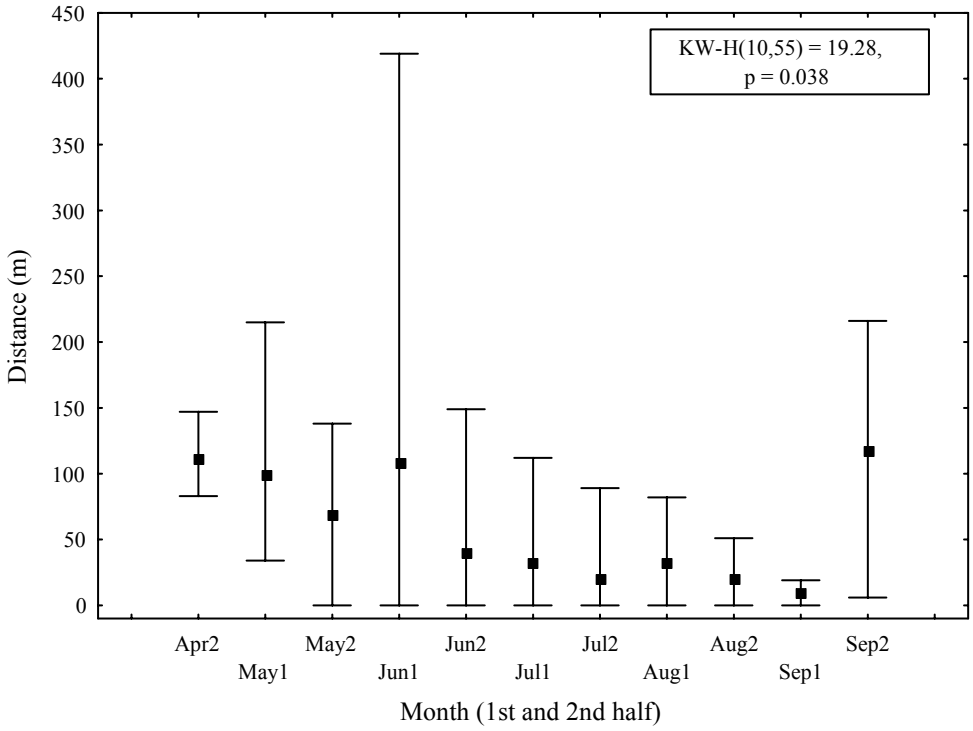


Figure 3.4 Seasonal movements for five *B. gabonica.* Boxes denote means, error bars denote min-max.

A seasonal looping pattern was observed for two individuals within their respective home ranges. Both snakes (one male, one female) were wild individuals released with implanted transmitters at their capture points, and both were tracked for nearly (Snake #6 - 328 days) or more than (Snake #1 – 504 days) a full seasonal cycle. After remaining in the same location for almost 3 months through the winter, snake # 6 moved southwest, then roughly to the east during the summer months, followed by northeast and northwest movements to end up, after 1.6 km of total movement, in the same activity centre (50% KD) and less than 75 m from the site it had occupied 10 months earlier (Fig. 3.5). Likewise, snake #1, a male, made a broad looping excursion of over 2.5 km through various

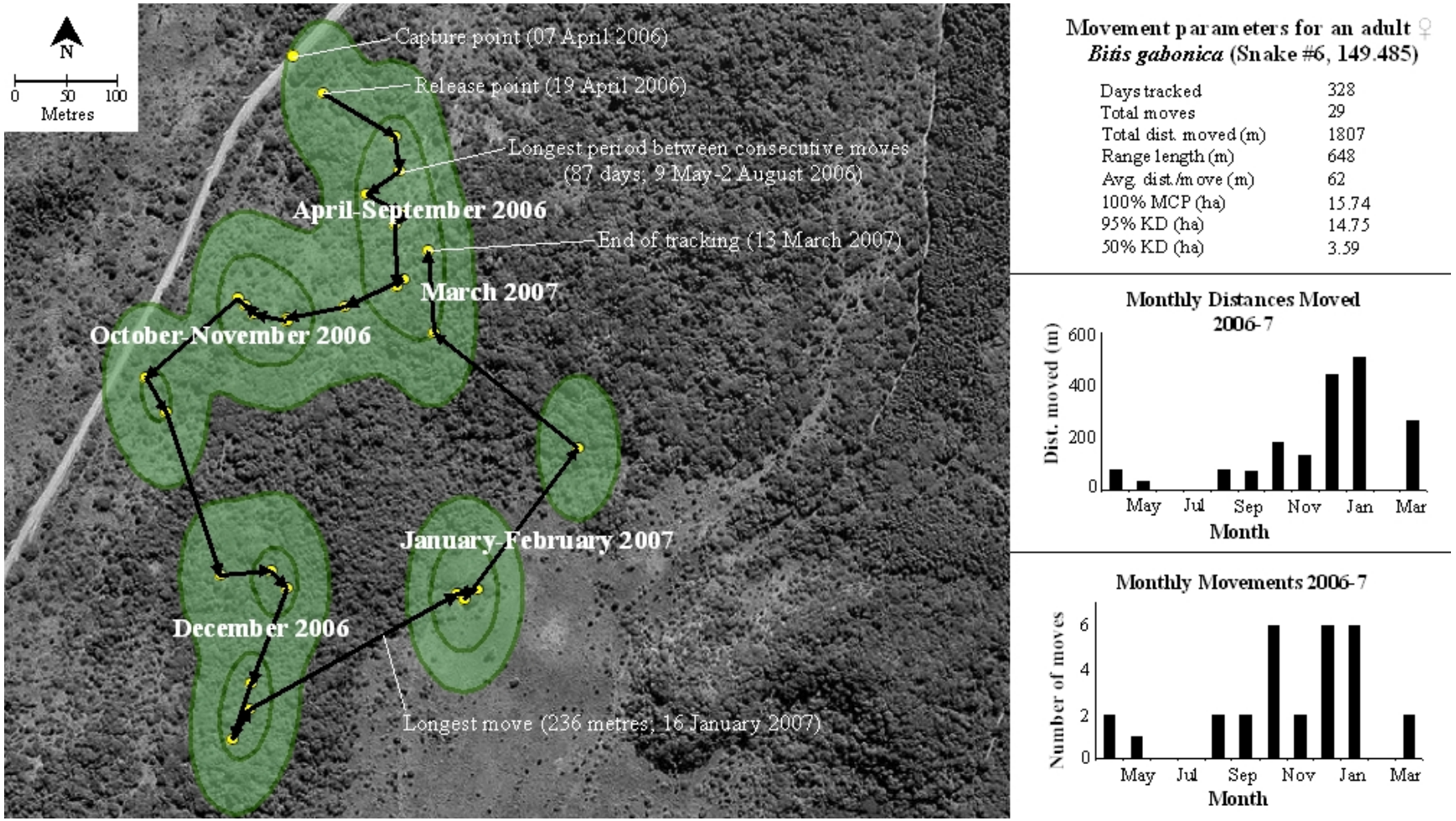


Figure 3.5 Activity pattern and monthly movement data for an adult female *B. gabonica* on the Eastern Shores of iSimangaliso

habitats and ended up in a thicket adjacent to and less than 50 m away from the site it had occupied one year earlier in late March, within the same activity centre it had utilized the previous fall.

3.3.4 Movement biology and behaviour

Although individual *B. gabonica* remained stationary for days and even months, they did reposition their bodies within small areas of < 1 m^2. It was not possible to quantify how often these local body adjustments occurred, because snakes could not be monitored continuously throughout the entire course of a day. Often individuals appeared to have not repositioned themselves for many days, based on the relative position of particular twigs or leaves which lay on top of the snake. At other times, it was observed that snakes actively repositioned themselves on a regular basis throughout the course of the day.

I interpreted minor adjustments to be largely a result of thermoregulatory needs. The most common strategy would be for snakes to select a site that provided a heterogeneous assemblage of vegetative cover densities so that it could shuffle portions of its body in and out of direct or dappled sunlight without moving itself to a new location (see Chapter 4 for habitat selection). The intensity of these micro-movements presumably fluctuated seasonally; minor adjustments appeared to decrease in winter, probably because on most days, it took a snake longer to raise T_b to the selected T_b and therefore longer times needed to be spent in positions of optimal sun exposure. Feeding levels among telemetred *B. gabonica* also decreased in winter (see Chapter 5), reducing the need for daily body adjustments related to foraging.

Although absolute frequency of body re-positioning could not be recorded, telemetry monitoring allowed for the types of *B. gabonica* body positions to be recorded and analyzed. Due to their terrestrial habits and relative small body length/girth ratio, individual *B. gabonica* are limited in comparison with other snake taxa in regards to body positioning. I categorized observed *B. gabonica* as either being in a “coiled” or “spring” position (Fig. 3.6). I classified a snake as coiled if its head and tail were close to each other, and in a spring position if its body contained s-bends and neck was tightly kinked (positioning usually associated with hunting; Chapter 5). Individuals were observed in

completely straight postures only during movement (1.30% of fixes); coiled and spring positions were recorded for 49.97 % and 48.73% of total observations, respectively.



A. “Spring” B. “Coil”

Figure 3.6 Body positioning for *B. gabonica*

Individual *B. gabonica* were frequently partially burrowed into the sandy substrate and/or leaf litter. In addition to observations of captive *B. gabonica*, burrowing movements were observed twice among telemetred snakes. On each occasion, after selecting a location, the viper would anchor its tail into a set position before slowly compressing the straightened body into a series of s-bends, starting from the posterior end. While “backing” into position, simultaneous downward wriggling movements of the body displaced the substrate until the snake had carved out a trough for itself, rendering the entire body flush with the ground (Fig. 3.7). Positioning of the head occurred last, which was never buried in the sand deep enough to cover the lower labial scales. All monitored individuals showed this burrowing behaviour, but frequency of burrowing was variable among snakes and dependent on habitat. While the majority (> 75%) of the upper dorsum was usually exposed in semi-burrowed snakes, exceptionally (five observations) the entire body (excluding the head) was covered. Impressions left by snakes after vacating sites could be clearly discerned.



Figure 3.7 *B. gabonica* partially burrowed in leaf litter. Note height of snake relative to substrate.

On rare occasions, telemetered *B. gabonica* were observed moving. They used rectilinear locomotion during these times. This technique uses the ventral scales for ground traction to propel the snake forward as underlying muscles pull its body along in a straight line. While capable of undulatory (serpentine) locomotion, many heavy-bodied snakes primarily employ rectilinear movements (Cundall 1987). For sedentary, rotund species such as *B. gabonica*, rectilinear movements are energetically less costly than other movement strategies (Walton et al.1990), and the species appears to have morphological adaptations such as wide ventral scales with large, unencumbered (unconnected to ventral costocutaneous muscles) edges to enhance control and "gripping" ability during these straight, caterpillar-like movements (pers. ob.).

During movement, telemetered *B. gabonica* proceeded at a very slow pace, with head raised above the substrate (< 45°) and tongue flickered frequently, accompanied by occasional side to side head movements. All movements were uni-directional (not meandering) and were punctuated by periods where the snake would remain motionless. The farthest movement observed was 18 m over the course of 50 minutes by Snake #1. On a separate occasion, I disturbed the same individual during movement, and it immediately assumed a typical "viper" defence position, with the anterior part of the body raised off the ground and cocked back in a striking position. After a few seconds, the snake resumed its locomotion as if undisturbed.

Probably a function of its slow locomotion, *B. gabonica* is nearly silent during movement, even when traversing leaf litter on the forest floor. Logs and dense thickets did not appear to be obstacles to movement and in one instance a telemetred female (#2) swam a width of 2 m across a flowing stream, although this was not observed directly. Apart from this isolated event, monitored *B. gabonica* were strictly terrestrial. Adult *B. gabonica* kept in captivity were unable to clear 1.5 m high walls surrounding their enclosure, and telemetered individuals never climbed into low vegetation to bask or forage (e.g. *B. arietans*; Branch and Branch 2004). *Bitis gabonica* always relocated to a different site after ecdysis (n = 11), perhaps to distance themselves from potential predators attracted by the sloughed material, or to avoid external parasites in the old skin that could reattach to the snake.

3.4 Discussion

3.4.1 Variation among individuals

Published activity data for snakes (see Reinert and Kodrich 1982; Moore and Gillingham 2006; Pearson et al. 2005; Whitaker and Shine 2003) show that most movement variables do not differ significantly between the sexes of various species, although some studies found significant differences between males and gravid females (Reinert and Zappalorti 1988; Marshall et al. 2006). My study was therefore similar to many ophidian spatial ecology studies in that significant differences were not found between males and females in general movement patterns. Extensive variation among individuals is the greatest handicap to empirically showing differences between

groups of individuals. This limitation can only be overcome by tracking a large sample size over a time period sufficient enough to reveal intraspecific differences in the spatial ecology of a species (Reinert and Zappalorti 1988). Though I was not expecting to find strong differences between *B. gabonica* groups due to my small sample size and trends among ecologically similar taxa, my analysis was also limited because the length of time tracked and the time of the year over which monitoring occurred was different among individuals; a common scenario when radiomonitoring free-ranging animals..

Significant differences were also not found in any movement category between wild and relocated *B. gabonica*. While some researchers report high levels of movement immediately following release of relocated *B. gabonica* (Lawson 2006; Bodbijl 1994), I did not observe this. Home ranges of relocated *B. gabonica* in this study did not axiomatically increase with the number of days tracked (Table 3.1), and the largest and smallest home range areas were observed from relocated individuals. With the exception of an adult female captured in uMtunzini and released with a radiotransmitter on the Eastern Shores, all other monitored relocates were captured in greater iSimangaliso. These snakes were relocated out of necessity (EKZNW management policy) because the locations at which they were captured (e.g. campsites, informal settlements) were considered unsuitable for their release. Relocated *B. gabonica* showed no obvious adverse effects following release, and behaved in a manner similar to resident snakes.

Relocation (translocation) endeavors are a controversial subject in herpetology from genetic, epidemiological, and ecological standpoints, and should not be done unless potential benefits outweigh possible negative consequences (King et al. 2004). Although spatial data from my study suggests that relocation of *B. gabonica* can be successful in some circumstances, because the issue is locally pertinent in South Africa due to historical translocation events (EKZNW unpub. data), it is dealt with comprehensively in Chapter 6 in the context of conservation management. Current EKZNW policy for relocating *B. gabonica* is detailed in the Appendix.

Home ranges were extremely small for some of the telemetered snakes, especially when considering activity centers alone (50% KDs). It is possible that these smaller home ranges underrepresented space use for selected *B. gabonica* because they were not tracked for full seasonal cycles.

Conversely, the home ranges of snakes #1, 4, and 5 were unexpectedly large. The difference between these individuals and other seemingly less vagile *B. gabonica* was not a function of differing ecological strategies (all *B. gabonica* were extremely sedentary after site selection), they simply had higher movement frequencies (utilized more sites) and moved longer distances between sites.

Data from my study are comparable with preliminary home range data for *B. gabonica*, with the exception of one male from a South African study (Linn et al. 2006) that occupied a home range of 576.60 ha (Linn et al. 2006). The authors attribute this enormous home range to large distances (11438 m in total) moved through marginal habitats during the mating season; however, this snake was translocated and it is likely this type of space occupancy is atypical of normal South African *B. gabonica* movement patterns.

During my fieldwork, few observations of movement occurred during the morning and afternoon hours, and nocturnal movement probably accounts for most site-relocations, at least during certain seasons. Angelici et al. (2000) observed that *B. gabonica* in Nigeria were more active during nighttime hours in the month of March. In early April, a female *B. gabonica* was captured for my study on a tar road at 11:50 p.m. Sky condition was clear, and the road temperature was 25 °C with 80% air humidity. Most observations of wild, free-ranging *B. gabonica* have been made during fall on roads in South Africa at night (pers. obs., Bodbijl 1994).

3.4.2 Seasonal movement patterns

Although variation in space use and movement among individual telemetered *B. gabonica* was observed, certain activity patterns and movement behaviours were clearly evident for all telemetered snakes. Most importantly, movement data showed an obvious seasonal activity pattern that was stronger than hypothesized. The bimodal pattern of bouts of activity in spring and fall seasons is similar to some North American species that disperse from hibernacula and move long distances in early spring, reduce movements in the summer, and increase activity again with the fall mating season. In South Africa, the explosion of movement associated with the fall mating season is well documented for *B. gabonica* (Bodbijl 1994, Linn et al. 2006), but other than the mention of possible

summer decreases in activity (Linn et al. 2006), no seasonal trends of *B. gabonica* movements have previously been published.

The seasonal activity pattern that I observed among South African *B. gabonica* both answers and raises interesting questions. Although South African *B. gabonica* are not very different genetically from other, more northern populations (see Chapter 6), this isolated, southernmost population is likely to be ecological distinct. The northern coastal plain where *B. gabonica* occurs in South Africa has hot, humid summers and cool, dry winters and is markedly different from tropical Africa, where clear wet and dry seasons occur, but ambient monthly temperatures do not strongly vary (Lawson 2006, Luiselli and Akani 1998). Although seasonal movements for tropical *B. gabonica* are not available for comparison, because of strong climatic differences, it is probable South African *B. gabonica* have adapted a unique activity pattern, primarily in response to the cooler Zululand winters. The extreme cessation of all activity (up to three months with no movement) during the winter by telemetered snakes in my study is interpreted to be a response to significantly lower ambient temperatures during this season compared to the rest of the year, and no such extreme inactivity has been recorded in studies outside of South Africa.

During winter, significant habitat shifts were observed along with activity decreases, with *B. gabonica* moving to open-canopy areas before long periods of winter inactivity (Chapter 4). Individuals probably opted for these sun-exposed sites rather than winter retreats (hibernacula) because thermal requirements necessitated constant passive basking throughout each photoperiod and outweighed the risks of snakes remaining exposed on the surface at one site for long periods of time. Extremely long winter periods with no movements but without affiliated hibernation events likely make South African *B. gabonica* the most sedentary non-brumating snakes in the world, at least during significant spans of their lives. Bushmasters (genus *Lachesis*), the New World viperid equivalent to *B. gabonica*, have been recorded immobile at the same location for up to 67 days, but this was probably related to hunting behaviour, and not a seasonal effect (H. Greene, pers. comm.).

3.4.3 Mating activity

Linn et al. (2006) suggested a promiscuous polygynous mating strategy for *B. gabonica*, with males undertaking long mate-searching movements for passive females. However, my data show activity peaks for both sexes during the mating season, and although I did not observe mating among wild *B. gabonica* (copulation purportedly lasts approximately 5 minutes; Akester 1979), I suggest that the mating strategy for the species needs to be re-interpreted, as it is likely female movement during the fall is associated with pheromone trail deposition. Barring extremely high population densities, it seems rational that females of a sedentary species like *B. gabonica* would face selective pressure for the development an attractant mechanism (the release of pheromones) if males are to find them. Angelici (2000) observed combat between males during the mating season in the wild (in apparent isolation from females) which also suggests that mate-searching males interact only because they are chemically trailing a common female. Alternatively, closed canopy habitats may have little wind to disperse pheromones, so movement of female *B. gabonica* during the mating season may be an adaptation that increases opportunistic encounters with mates.

In Nigeria, Luiselli et al. (1998) found gravid *B. gabonica* between May and July (early phase of the wet season), whereas copulation was observed in January and February (peak of the dry season). In all other studies across the distribution, mating of *B. gabonica* is purported to occur sometime during March-May, with females undergoing parturition approximately one year later during the same period, suggesting bi- and triennial breeding cycles (Akester 1979; Angelici 2000; Lawson 2006). For South African *B. gabonica*, this means gravid females likely forgo longer fall movements in some years because they are not sexually receptive to males.

The possibility also exists that mating for the species in South Africa is not limited to the fall season. From 24 October – 2 November 2006, a telemetered male *B. gabonica* (Snake # 1) moved 806 m (straight-line distances between sites, so this is number is likely an underestimate), including a single movement of 405 m to the inside of a thicket where he was subsequently observed with a female less than 1 m away. Based on the highly unusual preceding movement pattern and the proximity of the two snakes, mating was suspected but could not be verified because copulation was not observed. A semi-annual mating cycle would explain large distances moved during the spring by some individuals, although I also attribute spring increases in movement at least in part to increased feeding activity (active selection of ambush sites) after long winter periods where hunting behaviour

was not observed. The looping pattern observed in two snakes may also be related to mating, or it is possible that *B. gabonica* annually return to the same area to over-winter; both scenarios (if actual) strongly suggest that individuals do in fact have true home ranges.

3.4.4 Tolerance by B. gabonica to disturbance

Although capable of long movements and large home ranges, if there is a predominant theme that emerges in the life-history of *B. gabonica*, it is that these vipers are sedentary, spending very long periods of time at single sites. While most viperid species are sedentary and have "slow" life histories (Shine et al. 2003; Alexander and Marias 2007), because of its mild temperament, *B. gabonica* stands out in stark contrast even among members of its own genus (i.e. the irascible *B. arietans* and *B. atropos*). Extreme docility has a direct bearing on the spatial ecology of *B. gabonica* because the species' high tolerance of disturbance means that the majority of movement activity is facilitated from intrinsic biological requirements, not external stimuli.

This extremely inert, almost comatose behaviour was observed frequently during the monitoring of *B. gabonica*. As a rule, telemetered snakes were highly resistant to tactile and vibrational disturbance. On two occasions, I accidentally stepped directly on *B. gabonica* during the course of radiotracking, only becoming aware of this after feeling squirming movement beneath my foot. At no point during either encounter did the snake hiss or show aggression in any manner. In one of several similar incidences involving my field dog, his front paw stepped squarely on the head of a imperturbable Gaboon Adder thermoregulating at a thicket edge, then paused for several seconds before moving on, unaware of the snake. During locomotory activity, *B. gabonica* seemed unperturbed by my presence Angelici et al. (2000) also record similar instances involving moving *B. gabonica* that seemed to totally ignore humans in close proximity.

Bitis gabonica #5, a large male, had a notable encounter with Park personnel during the course of monitoring. On 19 June 2006, I observed the snake coiled at the base of a small (~2 m tall), invasive Guava tree (*Psidium* sp.). The following day, alien-bush clearers came through the area and removed the tree, cutting it several centimetres above the base, apparently oblivious of the snake's presence. On June 21st, during the course of tracking, I found the snake still in the same location, except now

covered by the felled tree. On several occasions, *B. gabonica* were observed < 5 m away from roads for periods of days, and the ambush hunting strategy and habitat preferences of the species frequently placed snakes partially on or near trails used by antelope (*Tragelaphus* sp.), hippopotamus (*Hippopotamus amphibious)*, and elephant (*Loxodonta Africana*). Fresh spoor from these large mammals was frequently observed in very close proximity (< 1 m) to occupied *B. gabonica* sites, and orange tape tied above *B. gabonica* to demarcate site locations for habitat analysis were occasionally nibbled on or chewed off by bushbuck (*Tragelaphus scriptus*) while the snake was still present at the site. On one occasion, a large leopard (*Panthera pardus*; identified from pug marks) walked through a small thicket that contained a motionless telemetred snake.

Owing to their corpulent form, camouflage, and potently venomous bite, adult specimens appear to have very few (if any) natural predators (Mallow et al. 2003); although neonates are discernibly more aggressive (pers. ob.) and one individual (excluded here from spatial analyses) was tracked for two weeks before death by predation. The absence of predation risk has wide-reaching ecological implications and further capacitates a lethargic life-history that does not invest significant energy into excessive self-protective behaviours (i.e. elaborate defence displays, fast movements to retreat sites). The placidity of *B. gabonica* is historically well documented (Mallow et al. 2003 and references therein), but the adaptive advantage of this strategy has not been examined in depth. In Chapter 5, I propose that many of the extreme morphological and behavioural characteristics observed in *B. gabonica* are the result of strong selective pressures on aspects of feeding ecology and behaviour.

3.5 Conclusions

Although sedentary for much of the time, *B. gabonica* are capable of moving long distances. Home ranges and movement statistics varied among individual *B. gabonica*, but for most movement parameters, males had higher averages. A definitive bi-modal seasonal activity pattern is evident for *B. gabonica* in South Africa, with movement peaks in spring and fall, inactive periods in winter, and to a lesser extent, late summer. The remarkable capacity to remain relatively motionless for months at a time during the winter months makes South African *B. gabonica* ecologically very distinct from other snakes, and possibly even from other *B. gabonica* populations. An underlying paradox is that

although *B. gabonica* are highly sedentary for long periods, they can still occupy large home ranges areas.

Mating activity elicits long movements during the fall by both sexes. Although it appears males move longer distances than females in mate-searching endeavors, contrary to previous findings, females also move greater distances during this time, probably to lay down pheromone trails. Future research is needed, though, into the frequency of mating and the length of gestational periods for *B. gabonica* in South Africa.

Extreme crypsis coupled with adaptive behaviours such as burrowing in leaf litter and high tolerance to various forms of disturbance enable *B. gabonica* to remain at single sites for long periods of time, and demonstrate how strong evolutionary pressures can be in developing species with "slow," yet successful life-history strategies. This analysis of the spatial ecology of *B. gabonica*, although limited in certain regards, represents the most comprehensive study of its kind for any African snake species, and hopefully will encourage future research initiatives into reptilian spatial ecology on the continent.

Chapter 4: Habitat use and selection strategies

4.1 Introduction and experimental approach

The iSimangaliso Wetland Park is a composite landscape of wetland, grassland, closed and open woodland, thicket, and forest vegetation types. These ecotypes provide habitat for an impressive diversity of species, many of which are of conservation importance (KZNNCS 1998). Although *Bitis gabonica* is a protected and well-known reptile in the region, reliable information pertaining to the use, selection, and importance of habitat for *B. gabonica* has been largely absent from the scientific literature, and perhaps more importantly, from current management plans that aim to protect the species in South Africa (EKZNW 2004).

Morphologically and ecologically well-adapted for life on the forest floor, *B. gabonica* is associated continent-wide with tropical and sub-tropical forests and immediately adjacent well-wooded savanna areas (Angelici et al. 2000; Bodbijl 1994, Lawson 2006; Luiselli and Akani 2003). Most of this habitat in South Africa exists as a narrow (100 m to several kms wide), linear stretch of coastal dune forest at the eastern extremity of the Mozambique coastal plain (Fig 4.1). Recordings exist from as far south as Umtunzini (28º57'S, 31º44'E) and inland as far as Manguzi (26º59'S, 32º45'E) and Matubatuba (28º25'S, 32º12'E) (Armstrong 2001; Bodbijl 1994). Like other reptile species found in South Africa with "tropical" distribution and ecological affinities, *B. gabonica* reaches its southern range limit near Umtunzini (Fig. 4.2), where the coastal plain tapers and disappears (Maritz 2007). The species' range extends north into southern Mozambique (Manhica is the most northern record) but there is a large disjunction (~ 450 km) between records in extreme southern Mozambique and records in northern Mozambique and eastern Zimbabwe.

The use of microhabitats within forests and forest mosaics, and why *B. gabonica* select these areas, are sources of speculation. In South Africa, previous research suggested that suitable habitat for the species was strongly correlated to prey availability, limiting individuals to the forest ecotone where densities of favored rodents were high (Perrin and Bodbijl 2001a). This study provided important

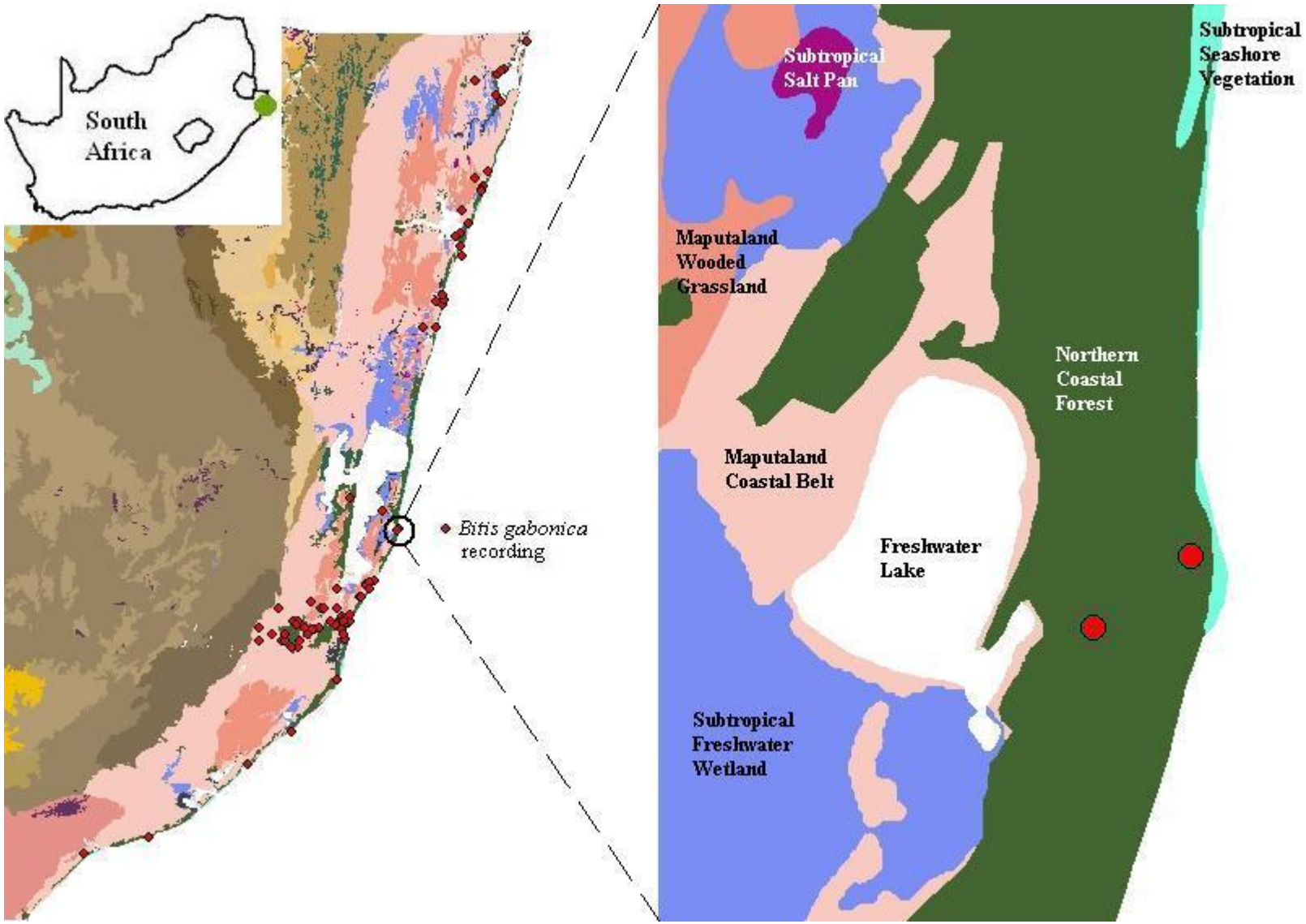


Figure 4.1. Association of *B. gabonica* with coastal forest habitat in South Africa. Red points represent all known historical recordings (n = 101) of the species in South Africa (sourced from the EKZNW Biodiversity Database, Transvaal Museum, Bodbijl (1994) and new records from this study). Unverified and anecdotal records are not represented. This map was created in ArcMap 9.2 using the most accurate SANBI vegetation maps and GIS shapefiles to date (Mucina and Rutherford 2006).

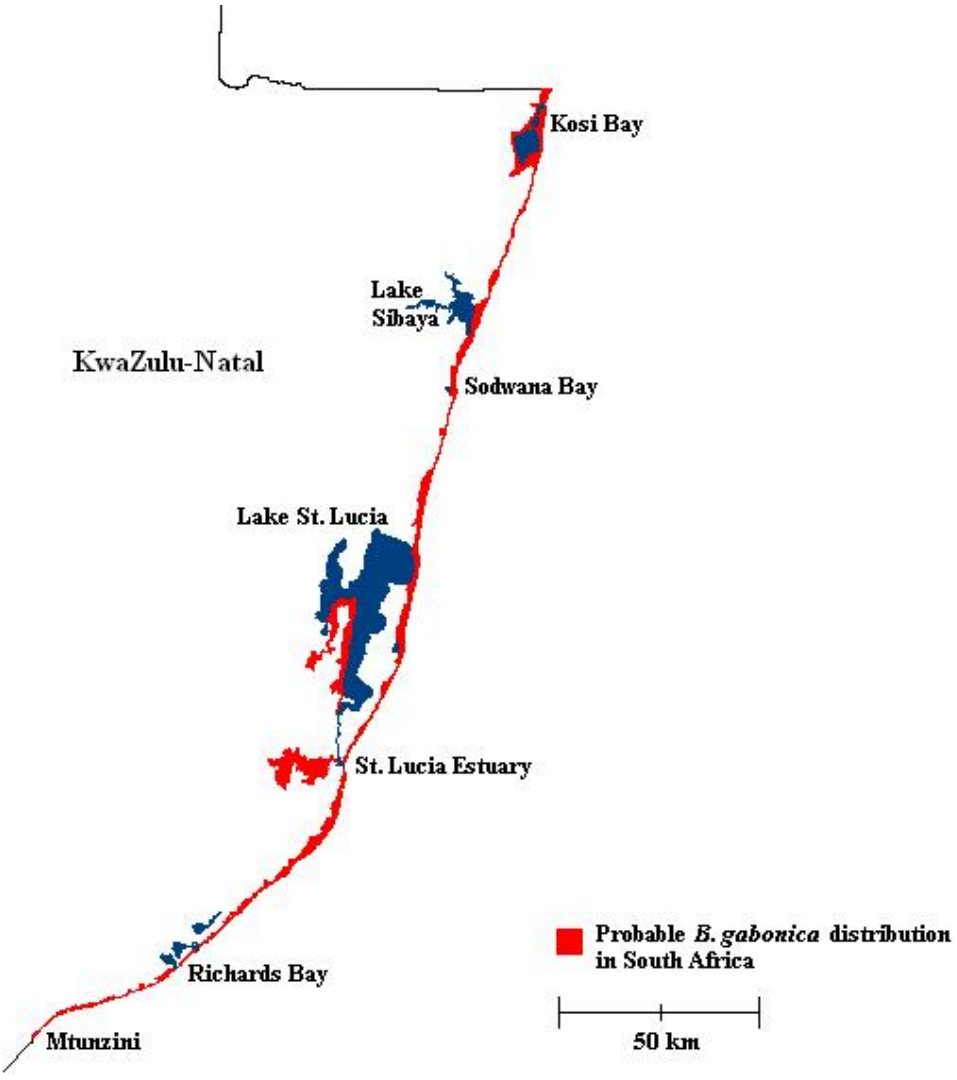


Figure 4.2 Interpreted South African *B. gabonica* distribution from historical distributional records and suitable macrohabitat ('Northern Coastal Forest', Mucina and Rutherford 2006).

insight into the diet of South African *B. gabonica* (Perrin and Bodbijl 2001b). However, the work of Bodbijl (1994) was limited in the number of monitored individuals and lacked quantitative habitat analyses. Because knowing the habitat of a species is critical to understanding its ecology, I specifically incorporated the inclusive and accurate identification and description of *B. gabonica* habitat as a major goal of my research.

Factors influencing snake habitat use include sex and reproductive condition, foraging and digestive state, ecdysis, disease and injury, social relationships, and site fidelity (Reinert 1992a). Snakes, like many other animals, select macrohabitat based on a combination of physiological factors, genetic programming, and basic habitat choices shaped by natural selection (Marshall et al. 2006; Moore and Gillingham 2006; Reinert 1992a). Within a given macrohabitat, individuals then select sites (microhabitats) using relevant structural, external environmental and chemical cues (Bevelander 2006; Orr 2006). The micro-heterogeneity of a species' habitat is the most difficult to classify and requires extensive monitoring and observation of individuals (Leyequien et al. 2007). Use of radiotelemetry to study wild snakes can help address the incongruence between actual and perceived patterns of snake habitat use (Reinert and Zappalorti 1988).

Because habitat characteristics are multidimensional, habitat studies need to include multivariate techniques that address the amalgamation of factors critical to the success of a species in a given area (Reinert 1984a). While it may be impossible to account for all the individual components that collectively constitute "suitable habitat," it is feasible in many cases for the field researcher to establish which habitat variables are most important to a species (Reinert 1992b). In recent snake habitat studies, these critical factors have been identified for different species and populations by comparing a standardized set of habitat variables at locations actually selected by snakes and at corresponding random sites in the same area (e.g. Moore and Gillingham 2006; King et al. 2004; Reinert 1984b). Sites in the two groups are then compared to determine which variables are primarily associated with the variance between the groups. The defining characteristics of snake sites are then used to describe the specific habitat that individuals of a species are selecting and how assessable the microhabitat is within the home range of those individuals.

Here, I follow a similar experimental approach in order to establish which features are important in the habitat selection process for South African *B. gabonica*, and how the areas that individuals use

differs from the characteristics of the landscape in general. I also extend my analysis to examine seasonal differences in habitat use as well as differences in habitat selection between males and females in producing a robust definition of "suitable habitat" for *B. gabonica* in South Africa.

4.2 Materials and Methods

4.2.1 Habitat variables: description and measurement

To understand the habitat preferences and selection strategies of *B. gabonica* in South Africa, I gathered data from ten telemetered, free-ranging *B. gabonica* (six males and four females) within iSimangiliso from 2005-2007 (detailed radiotelemetry methodology is provided in Chapter 2). After a telemetered snake had moved to a new location, I marked the location of the site with vinyl flagging tape and revisited the locality for habitat analysis subsequent to the individual moving out of the area. For purposes of habitat analysis, a site was classified as 'new' when the snake had moved a minimum linear distance of 2 m from the previous site (as opposed to 5 m for spatial analysis because of GPS positional error). If a snake was found at the same site for consecutive observations, the habitat variables measured for that site were assumed to be constant for the duration that the individual remained at that location. Habitat site categorization and methodology used were similar to other studies (e.g. Whitaker and Shine 2003; Weatherhead and Charland 1985).

I hypothesized that the selection of macro- and microhabitat was interdependent, so I employed a hierarchical approach in selecting quantitative habitat variables to describe *B. gabonica* habitat in comprehensive terms. I chose 16 principal habitat variables that could influence *B. gabonica* habitat use, ranging from the landscape scale (macrohabitat) to the more immediate structural characteristics of microhabitat (Table 4.1). My variable selection process was guided by similar published snake habitat studies (Harvey and Weatherhead 2006; Moore and Gillingham 2006; King et al. 2004), but appropriate adaptations were made for the environment (i.e. "% rock cover" was replaced with "% leaf litter cover"). To standardize observer bias, I conducted all habitat measurements myself.

Microhabitat variables were measured within a 1 m^2 quadrant according to standardized sampling methods (Ratti and Garton 1994), with the quadrant positioned so that the snake location was at the centre. Measures of distance of the structural features ≤ 1 m from the location of the snake were

rounded to the nearest 0.1 m. Measures of distance of the structural features ≥ 1 m from the snake were rounded to the nearest 0.5 m. Distances were measured with a Keson® 30 m measuring tape. Distances over 30 m were measured by a Bushnell® YardagePro laser rangefinder.

Table 4.1 Structural habitat variables measured at each *B. gabonica* and random site

Mnemonic	Habitat variable	Variable explanation	Scale
CS1	Overhead canopy structure	Average openness (%) of overhead canopy measured by densiometer	1 m^2 quadrant
CS2	Understory canopy structure	Understory coverage categorized by score (1-5)	1 m^2 quadrant
WSD	Woody stem density	Total number of woody plants	1 m^2 quadrant
DWS	Distance to nearest woody stem	Distance (m) to nearest woody vegetation	20 m radius
TD	Tree density	Total number of trees (≥ 75 mm dbh [diameter at breast height])	1 m^2 quadrant
DT	Distance to nearest tree	Distance (m) to nearest tree (≥ 75 mm dbh)	50 m radius
LOGD	Log density	Total number of logs (≥ 75 mm at greatest width)	1 m^2 quadrant
DLOG	Distance to nearest log	Distance (m) to nearest log (≥ 75 mm at greatest width)	20 m radius
GLIT	Leaf litter cover	Leaf litter ground coverage (%)	1 m^2 quadrant
GH20	Water cover	Water ground coverage (%)	1 m^2 quadrant
GSAND	Sand cover	Sand (bare substrate) ground coverage (%)	1 m^2 quadrant
GVEG	Vegetation cover	Live vegetation ground coverage (%)	1 m^2 quadrant
GLOG	Log cover	Log (≥ 75 mm at greatest width) ground coverage (%)	1 m^2 quadrant
GTREE	Tree ground cover	Tree (≥ 75 mm dbh) ground coverage (%)	1 m^2 quadrant
HAB	Macrohabitat type	1 = forest, 2 = ecotone, 3 = woodland, 4 = grassland	10 m radius
DEDGE	Distance to habitat edge	Distance to nearest different macrohabitat or road	50 m radius

Overhead canopy cover was measured within each quadrant by concave spherical densitometer (Forestry Suppliers, Inc.). This handheld instrument uses a spherical-shaped reflector mirror engraved with a cross-shaped grid of 24 quarter-inch squares. Readings are taken by holding the densiometer level approximately 400 mm in front of the body at elbow height. Four equi-spaced dots in each square of the grid are assumed and systematically counted, and then the total count is multiplied by 1.04 to obtain the percent of overhead area not occupied by canopy. Therefore the values reported here for overhead canopy structure reflect the degree of canopy openness, not coverage. Four readings in each cardinal direction were taken at the location of the snake in each quadrant and the average recorded.

To assess understory canopy structure, I considered the total area within each 1 m^2 quadrant up to a height of 1 m (in essence a 1 m^3 cube over the location of the snake). I then assigned the given site a score of 1-5 based on how dense the herbaceous layer and woody vegetation of the quadrant was, or how much the understory "filled" the cube. If a 1 m^3 cube is imagined, a score of 1 means that cube is 0-20% full; 2 = 20-40%, 3 = 40-60%, 4 = 60-80%, 5 = 80-100%. A snake site located inside a dense, impenetrable thicket would usually merit a score of "5", while a site in open forest floor with little or no vegetation would receive a "1". Essentially, the purpose of this variable was to describe the "shrubbiness" of a site.

Telemetered snakes utilized three distinct macrohabitats: forest, wooded grassland, and grassland. Although forested habitat in iSimangaliso can be botanically subdivided into dune forest, coastal lowland forest, and swamp forest, I treated all forested areas as one macrohabitat due to shared structural similarities and use by *B. gabonica* (KZNNCS 1998). I also included "forest ecotone" as a macrohabitat because of its structural uniqueness and presupposed importance to *B. gabonica* habitat use (see Linn et al. 2006; Perrin and Bodbijl 2001a; Bodbijl 1994). I designated telemetered *B. gabonica* as having occupied the ecotone if the snake location was ≤ 5 linear metres of either side of the forest treeline. While floristically, the forest ecotone is wider than the 10 m buffer I classified as "edge" habitat (Armstrong 2002), structurally this width was a realistic estimation of ecotone width at my study site. I scored macrohabitat as following: forest =1, ecotone = 2, wooded grassland = 3, grassland = 4. These rankings also correspond to the average canopy cover of a given macrohabitat relative to the other three, with forest (1) being the most closed and grassland (4) having no overhead canopy cover. Categorization and measurement methodology for random sites was identical to *B. gabonica* sites.

4.2.2 Statistical analyses

I tested for differences among habitat characteristics of individual *B. gabonica* sites using MANOVA for three variables: season, sex and habitat selection. I chose random sites for habitat analysis by randomly selecting 50 GPS waypoints found within the collective home range area (95% kernel density contours) used by all telemetered *B. gabonica*. In like manner to my seasonal movement analysis, I designated "winter" *B. gabonica* sites as localities occupied by snakes in the months of

June-August, and "non-winter" sites as localities occupied during all other months. If a significant difference was found for a group ($p \leq 0.05$), I examined the Sum of Squares within the MANOVA model in order to determine which measurements were most responsible for the significance result (what variables explained the variability between cohorts). For season, sex and habitat selection groups, I grouped together all individual measurements in my analysis when making comparisons between groups. My statistical methodology is identical to that of other published snake habitat studies (King et al. 2004; Reinert 1992a) and accordingly aims to reflect the ubiquitous habitat selection trend of the species, as opposed to focusing on minor variation among individuals. All statistical analyses were performed using Statistica ver. 6 (2002).

4.3 Results

Habitat variables were collected at 658 *B. gabonica* sites and 50 random sites, for a total of 11328 measurements used in my habitat analysis. 308 (46.8%) of the snake sites were sites only used once before the individual relocated (the remaining sites were locations individuals were recorded at more than once, and for these sites the habitat variables measured were assumed to be constant for the duration that an individual remained at that location). MANOVA determined significant difference among summer and winter sites (Wilks' $\lambda = 0.77$, $F(16,641) = 12.14$, $p < 0.001$), male and female sites (Wilks' $\lambda = 0.71$, $F(16,641) = 15.99$, $p < 0.001$), and snake and random sites (Wilks' $\lambda = 0.89$, $F(16,691) = 5.32$, $p < 0.001$). Within each cohort, there was no single habitat variable that could explain the difference between types of sites sufficiently (no single characteristic of habitat explained $\geq 50\%$ of the total variability). Rather, a combination of top-ranking variables described the differences among the seasonal, sex and habitat groups.

Although underground retreat sites are purportedly utilized by other populations of *B. gabonica* (Angelici et al. 2000; Lawson 2006), individuals in my study were strictly terrestrial. Telemetered *B. gabonica* used different habitats in the winter months to those selected during the rest of the year, with snakes utilizing open habitats (areas of greater sun exposure) during the cooler winter period (Fig. 4.3). Among summer and winter sites, macrohabitat was the best predictor of site type (28.99% of the total variability, Table 4.3) with non-winter sites structurally closer to forest (mean = 1.59, Table 4.2) than winter sites (2.43). Overhead canopy structure (variance = 21.60%) was on average

almost twice as open among sites used in winter (47.51) than among non-winter habitat (25.31). Ground litter (variance = 11.19%) was the third most important characteristic separating seasonal sites, with the remaining seven significant variables individually contributing less than 10% to the total variability.

Table 4.2 Means ± standard errors of habitat variables for six groups. *n* = number of sites

Variable	Non-winter (*n* = 491)	Winter (*n* = 167)	Male (*n* = 372)	Female (*n* = 286)	Snake (*n* = 658)	Random (*n* = 50)
CS1 (%)	25.31 (1.35)	47.51 (2.32)	31.32 (1.63)	30.45 (1.86)	30.94 (1.22)	30.08 (4.44)
CS2 (1-5)	2.75 (0.06)	2.47 (0.11)	2.56 (0.07)	2.84 (0.08)	2.68 (0.05)	1.60 (0.20)
WSD (no.)	7.31 (0.23)	5.46 (0.40)	6.13 (0.27)	7.76 (0.31)	6.84 (0.20)	3.14 (0.73)
DWS (m)	1.55 (0.13)	0.24 (0.23)	0.50 (0.15)	2.16 (0.17)	1.22 (0.14)	2.38 (0.50)
TD (no.)	0.09 (0.01)	0.05 (0.02)	0.09 (0.02)	0.07 (0.02)	0.08 (0.01)	0.08 (0.04)
DT (m)	4.98 (0.37)	8.93 (0.64)	7.50 (0.43)	4.01 (0.49)	5.98 (0.32)	3.94 (1.16)
LOGD (no)	0.14 (0.02)	0.14 (0.03)	0.14 (0.02)	0.15 (0.02)	0.14 (0.02)	0.32 (0.06)
DLOG (m)	4.01 (0.17)	2.57 (0.29)	3.73 (0.20)	3.53 (0.23)	3.64 (0.15)	4.17 (0.56)
DEDGE (m)	35.40 (0.90)	32.72 (1.54)	33.97 (1.03)	35.70 (1.18)	34.72 (0.77)	39.90 (2.80)
GLIT (%)	49.83 (1.50)	32.13 (2.58)	41.87 (1.76)	49.84 (2.01)	45.33 (1.34)	44.80 (4.87)
GH20 (%)	0.12 (0.03)	0.00 (0.05)	0.00 (0.03)	0.21 (0.04)	0.09 (0.03)	0.00(0.09)
GSAND (%)	6.53 (0.64)	7.57 (1.10)	6.37 (0.74)	7.34 (0.84)	6.79 (0.57)	11.30 (2.08)
GVEG (%)	40.84 (1.58)	56.74 (2.72)	48.92 (1.84)	39.60 (2.10)	44.87 (1.40)	40.40 (5.06)
GLOG (%)	1.71 (0.35)	2.63 (0.60)	1.40 (0.40)	2.66 (0.46)	1.95 (0.31)	3.00 (1.11)
GTREE (%)	0.68 (0.17)	0.93 (0.29)	1.13 (0.19)	0.24 (0.22)	0.74 (0.14)	0.40 (0.51)
HAB (1-4)	1.59 (0.04)	2.43 (0.07)	1.82 (0.05)	1.77 (0.05)	1.80 (0.04)	1.62 (0.14)

Differences between male and female sites were best described by microhabitat characteristics, with proximity to woody vegetation and trees accounting for > 50% of the total variance (Table 4.4). On average, females selected sites further from woody vegetation (2.16 m) than males (0.50 m), but closer to mature trees (4.01 m and 7.50 m, respectively). Female sites were generally located in vegetatively-sparse areas of the forest, while habitat means for males show those individuals preferred areas that were slightly shrubbier.

Microhabitat variables were also the best distinguishing factors in separating random sites from *B. gabonica* sites. Random sites had thinner understory structures (1.60) than snake sites (2.68), and on average were farther away from (2.38 m) and had less (3.14) woody vegetation than *B. gabonica* sites (3.14 m and 6.84, respectively). Together these three variables explained almost 90% of the model variability (Table 4.5). The average random site was located in the open forest floor and characterized by a moderate to high percentage of leaf-litter ground cover, whereas most *B. gabonica* localities were inside or adjacent to thickets of varying sizes and vegetative densities.

Table 4.3 Explained variability among habitat variables of two groups: winter and non-winter sites used by telemetered B. gabonica

Variable	% Variability	F	p
HABG (1-5)	28.99	97.51	0.00
CS1 (%)	21.60	68.40	0.00
GLIT (%)	11.19	35.16	0.00
DT (m)	9.03	28.31	0.00
GVEG (%)	8.16	25.56	0.00
DWS (m)	7.85	24.61	0.00
DLOG (m)	5.82	18.34	0.00
WSD (no.)	4.99	15.81	0.00
CS2 (1-5)	1.28	4.75	0.03
GH20 (%)	1.09	4.17	0.04

Table 4.4 Explained variability among habitat variables of two groups: male and female sites

Variable	% Variability	F	p
DWS (m)	35.96	53.60	0.00
DT (m)	19.68	28.77	0.00
GH20 (%)	11.00	16.24	0.00
WSD (no.)	10.59	15.67	0.00
GVEG (%)	7.39	11.17	0.00
GTREE (%)	6.10	9.36	0.00
GLIT (%)	5.77	8.91	0.00
CS2 (1-5)	3.49	5.76	0.03
GLOG (%)	2.44	4.33	0.04

Table 4.5 Explained variability among habitat variables of two groups: *B. gabonica* and random sites

Variable	% Variability	F	p
CS2 (1-5)	40.39	27.44	0.00
WSD (no.)	34.89	23.73	0.00
DWS (m)	13.16	9.41	0.00
LOGD (no.)	6.25	4.96	0.03
GSAND (%)	5.31	4.37	0.04

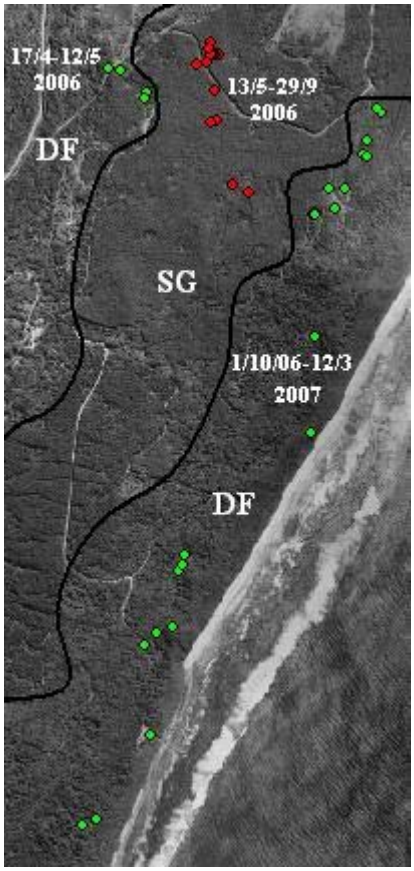


Figure 4.3 DF=Dune Forest, SG= Secondary Grassland. This figure depicts the differences in seasonal macrohabitat use by *B. gabonica*, showing the sites (represented by GPS points) selected by Snake #5 (tracked 4/06-3/07) as an example. This individual spent the winter in a grassland area immediately northwest of Mission Rocks (red points) and most of the non-winter months in dune forest (green points). At the time of this aerial photograph, the area demarcated as SG was a *Pinus* plantation but was not when utilized by the snake (photo EKZNW).

4.4 Discussion

4.4.1 Seasonal macrohabitat selection

My analysis of habitat selection by telemetered *B. gabonica* in South Africa suggests a seasonal shift in macrohabitat use by individuals of the species. During warmer months when *B. gabonica* is active, snakes select coastal lowland and dune forest habitats, or adjacent areas of mature wooded grasslands (Fig. 4.5). Here, *B. gabonica* can exploit transient patches of sunlight by strategically positioning themselves in microhabitats where they can manipulate portions of their bodies to bask or shuttle over small distances (< 1 m) between sun and shade. During winter, activity decreases

significantly, to the extent that many individuals do not move for extended periods (Chapter 3). During this time, *B. gabonica* employ a tactic closer to thermoconformity in open-canopied habitats that are fully exposed to sunlight for the entire day (Fig. 4.4). These areas include hydromorphic and dry grassland habitats bordering forested areas, open areas of wooded grassland, and forest clearings with high proportions of the forest floor exposed to sunlight.

The thermoregulatory strategies of terrestrial ectotherms in forested habitats range from passive thermoconformity to homeothermy (Fitzgerald et al. 1993). While passive thermoconformity may arise if precise thermoregulation is not possible or not needed (e.g. some nocturnal and tropical species; Vitt et al.1997), if the benefits outweigh the risks, many ectotherms will actively thermoregulate to attain selected body temperatures. However, species may alter the manner and type of thermoregulation based on daily and seasonal changes in ambient factors (Hertz et al. 1993), as appears to be the case with South African *B. gabonica*. In cooler months, while *B. gabonica* may not achieve selected body temperatures for significant portions of the day, they are able to reach the maximum temperature possible while maintaining low activity levels. In hot weather, individuals can maintain relatively high, constant body temperatures, also without compromising their highly sedentary behaviour. In each scenario, the species' preferred thermal strategy is facilitated by an appropriate selection of macrohabitat. I did not study *B. gabonica* thermal biology *per se* (e.g. Alexander 2007; Pearson et al. 2003; Shine et al. 2003), but my results suggest macrohabitat selection is closely linked to the seasonal thermal requirements of the species.

Taking the seasonal habitat shifts I observed into consideration, the ecology of sub-tropical *B. gabonica* near the southern margin of the species' range is likely different than the ecology of *B. gabonica* over the rest of its distribution. Primarily a tropical reptile, it is improbable that thermal consequences play a primary role in habitat selection for *B. gabonica* in equatorial Africa where environmental temperatures are generally high and do not vary widely on a seasonal basis. Although this assumption needs to be corroborated by field research, preliminary observations by some authors (Angelici et al. 2000; Lawson 2006) indicate that seasonal habitat shifts in more northerly *B. gabonica* populations are absent.



Figure 4.4 Examples of *B. gabonica* winter habitat: secondary grassland and forest edge. Note lack of overhead canopy cover.



Figure 4.5 Examples of *B. gabonica* non-winter habitat: thickets within interior coastal forest.

4.4.2 Influences on microhabitat selection

No single habitat variable in any of my analyses was dominant in the sense that by itself it was able to strongly predict or describe site type; a reflection of the structural heterogeneity of *B. gabonica* habitat. However, at the microhabitat scale, habitat characteristics were interrelated: a high percentage of leaf litter at a given site was usually associated with a high degree of canopy coverage, dense understory structures were often the result of high densities of woody vegetation, etc. Individual features of the immediate spatial environment were only relevant to the description of a site if they were included as part of a compilation of significant habitat variables. I suggest that these interlinked variables show site selection by *B. gabonica* at the scale of microhabitat is driven primarily by an individual's food acquisition, protection, and thermal requirements. A selected site is therefore invariably a trade-off between and an attempt to optimize these three essential factors.

Despite a pronounced difference in overhead canopy coverage between winter and non-winter sites, the understory structure was strikingly similar (non-winter = 2.75, winter = 2.47). What this means in terms of microhabitat selection is that *B. gabonica* select sites throughout the year that are structurally similar at the understory and herbaceous level (Fig. 4.6), without compromising the amount of required sunlight (radiative heat) penetrating the overstory canopy. While readily available within coastal forests, understory thickets and shrubs do not feature predominately among *B. gabonica* winter habitat of open woodlands and grasslands (KZNNCS 1998; pers obs.). However, *B. gabonica* still target these areas during the winter period because of the protection and crypsis they afford.

Given that adult *B. gabonica* are vulnerable to very few natural predators because of their highly effective camouflage and fearsome envenomation capabilities (Mallow 2003), the greatest danger to these sedentary vipers within iSimangaliso is most likely being inadvertently stepped on by ungulates such as *Hippopotamus*, large antelope species (*Tragelaphus* sp.), buffalo (*Syncerus caffer*) and elephant (*Loxodonta africana*). Individuals minimalize this threat in open winter habitats by selecting small thickets, dense grass tussocks intertwined with thorny vegetation, and even invasive guava shrubs (*Psidium* sp.); all microhabitats of limited overhead exposure that are isolated from established trails that larger animals utilize.

During the warmer months when suitable understory microhabitat structural features (e.g. *Isoglossa* thickets) for protection and thermoregulation are abundant in forested habitat, site juxtaposition to areas of prey use is prioritized in the microhabitat selection process (Fig. 4.7). Protection and thermoregulation still factor into site selection, but are not as critical during warmer months because of the superior structural heterogeneity coastal forest affords over more open habitats like grassland and woodland. *Bitis gabonica* does not actively hunt during winter months (Chapter 5), eliminating the need to select sites during this period based on feeding requirements, and allowing individuals to remain immobile at single, secure locations for months at a time (Chapter 3).



Figure 4.6 Understory and herbaceous-layer woody vegetation as protection for *B. gabonica*.



Figure 4.7 Structure of a *B. gabonica* site inside coastal dune forest. The snake is located on the forest floor directly beneath the orange flagging tape. Note active mammal run to the left, transient patches of sunlight, and protective understory.

Another factor that can affect *B. gabonica* microhabitat selection is interspecific competition. Luiselli (2006a,b,c) presents compelling evidence that competition for food between sympatric *B. gabonica* and *B. nasicornis* forces the two species to partition the spatial niche axis by selecting different microhabitats. However, such a situation is absent among southern African *B. gabonica* populations where *B. nasicornis* does not occur. *Bits gabonica* is the only large terrestrial viperid found in subtropical forests (*B. arietans* does not occur in forested habitats [Branch 1998, pers. obs.], despite exhibiting a high degree of ecological plasticity throughout other African ecotypes), and is presumably not in direct competition with other ophidians.

The influence of intraspecific competition (if such competition exists) on *B. gabonica* site selection in southern Africa is not well understood. In east Africa, limited ecological research has been undertaken for the species, but pioneering African snake enthusiast C.P.J. Ionides noted that in 1961 "my catches included 435 gaboon vipers," and that he "once found three gaboon vipers curled up together in a heap and caught the lot" (Isemonger 1968). Although *B. gabonica* population densities are probably not as high in South Africa as observed for other parts of the distribution (see Luiselli 2006c), during my field work, on two occasions I observed two *B. gabonica* sharing the same thicket (< 1 m apart). The first observation (June) was of a telemetred adult male with a male neonate, and the second was of the same adult male with an adult female (November; possibly because of mating activity). While *B. gabonica* is not gregarious, these observations and others (Luiselli 2006c, Isemonger 1968) are evidence that individuals can occur in very close proximity to each other under some circumstances. However, the dynamics of competition between individuals for resources are unknown and require further research.

4.4.3 Differences between site categories

Statistically, male and female *B. gabonica* sites were different, but most of the variance was attributable to differences between mean distances of group locations to microhabitat structural features like trees and woody vegetation. During radio-monitoring, these differences were subtle and I was not aware of them in the field. Captive and wild gravid *B. gabonica* show increased heliothermic behaviour (Akester 1979; Luisell 2006c; pers. ob.), which would presumably alter microhabitat use. However, under- and overstory canopy structures were not significant variables in

distinguishing male and female sites, so there did not appear to be a thermal advantage to the sites females were selecting. Additionally, none of the females that I monitored appeared to be gravid (although to minimize disturbance of natural behaviour I did not do regularly palpate females for embryos). There is no clear explanation for why female *B. gabonica* monitored during this study used slightly less shrubby microhabitats than males.

The difference found between *B. gabonica* sites and random sites is primarily explained by features that constitute the understory, with snake sites having denser understory structures and being located closer to woody vegetation. This is not surprising, given the importance of this type of "thicket" microhabitat to the protection, thermoregulation and food acquisition requirements of individuals. While these thickets are a defining feature of coastal lowland and dune forest ecosystems, areas of open floor are equally (if not more) abundant and widespread spatial attributes in forested habitat of northeastern South Africa (KZNNCS 1998; Bruton and Cooper 1980), and this was reflected at my study site. Therefore, it was not surprising that the majority of random sites I analyzed contained extensive portions of open forest floor within 1 m^2 quadrants; habitat uncharacteristic of what was selected on average by *B. gabonica*. However, as a caveat to interpreting the data, I characterized random sites at only 50 locations. While this number of measured random sites has been sufficient in other snake habitat studies (King et al. 2004), I hesitate to make sweeping assumptions about *B. gabonica* microhabitat availability from data collected at my study site, especially over the entirety of the species' South African distribution where coastal forest is spatially and structurally very heterogeneous (Van Aarde et al. 1996).

4.5 Conclusions

Habitat selection by *B. gabonica* in South Africa is hierarchical. Landscape-scale habitat preferences are strongly influenced by season, with individuals selecting open-canopied macrohabitats such as wooded and secondary grassland and forest edge in winter, presumably because forested habitats *B. gabonica* utilize the rest of the year are not adequate for the species' thermoregulatory requirements during winter. Microhabitat features, with the exception of overhead canopy cover, are structurally similar among sites selected in both winter and non-winter months. These sites are generally located close to woody vegetation (shrubs or thickets) and have a protective advantage over more exposed

areas. Mature thicket (dense shrubbery in the understory under which little or no vegetation grows) is a critical aspect of *B. gabonica* habitat and probably provides feeding, thermoregulatory, and protective advantages to individuals over other structural features available within the same macrohabitat. Although *B. gabonica* utilize a wider range of habitats than was previously assumed, further research is needed to evaluate the availability of microhabitat over the species' range in South Africa. The protected coastal forests of iSimangaliso Wetland Park, particularly the dune forest corridor, are important to the long-term viability of the species in South Africa.

Chapter 5: Foraging ecology, diet and feeding adaptations

5.1 Introduction

The process of food acquisition directly influences, and often strongly characterizes a species' ecology. The common names of snakes often allude to the centrality of feeding preferences (e.g., Egg-eaters; *Dasypeltis* spp., Slug-eaters; *Duberria* spp., Centipede-eaters; *Aparallactus* spp.) and foraging-related adaptations (e.g. Wolf Snakes; *Lycophidion* spp.) in the ecology and life history of species. Current herpetological theory assumes that the vast evolutionary radiation of snakes, observable within the fossil record and among extant taxa, was triggered by the adaptation of highly kinetic jaws, allowing snakes access to a greater variety of prey options, and therefore ecological niches. Today, much diversity of the advanced, or Macrostomatan ("large-gaped") snakes, is explained by species-specific morphological features involved with subduing and ingesting prey. It is therefore suspected that a prominent variable throughout the evolutionary history of snakes has been strong selection on traits involved with feeding (Greene 1997; Rodgriguez-Robles 1999).

The evidence of selective pressures on feeding related characteristics is unmistakable in modern snake genera where species have evolved observable adaptations for specialized feeding on one type of prey (e.g. termites, eggs). The diverse Atractaspididae is an excellent example of this, with each species being characterized by small heads and slender bodies, but exhibiting an array of species-specific cranial modifications (e.g. "side-stabbing" dentition, quill-shaped heads, undercut jaws) for feeding on fossorial squamates in narrow burrows (Shine et al. 2006a). Many other taxa are feeding generalists that don't exhibit charismatic morphological traits related to food acquisition, but nonetheless have very effective adaptations for killing and consuming prey. Powerful constriction and potent venom are examples of successful adaptations used to kill large and/or fast prey items that would otherwise be unobtainable (Greene 1997).

Groundbreaking studies (Aubret and Shine 2007; Keogh et al. 2005; Aubret et al. 2004) on Australian tiger snakes (*Notechis*) have recently demonstrated that both environment and genetics directly influence the morphology of snakes. For example, individuals that repeatedly encounter

large prey items can undergo marked increases in head and body sizes within their lifetimes (relative to conspecifics that feed on smaller prey in the same or a different population) to meet local feeding demands. Additionally, the individuals of a given population that are persistently exposed to larger prey accumulate gene mutations that specify for larger head and body sizes in subsequent generations; illustrating the importance of both developmental plasticity and genetics, and "the impossibility of dividing phenotypic variation into simplistic categories of 'nature' and 'nurture'" (Aubret and Shine 2007; Keogh et al. 2005; Aubret et al. 2004). While these studies likely depict a common—or even fundamental—biological concept, most snake taxa still await study to determine the effect of the relationship between genetics and environment on phenotype.

5.2 Approach, hypothesis generation and methodology

Research on captive-born *Bitis rhinoceros* (sister species to *B. gabonica*) by Bonnet et al. (2001) showed that body proportions of individuals can be influenced by their environment after birth. In the study of Bonnet et al. (2001), accelerated and larger growth of anatomical features involved with feeding was observed among individuals that were fed larger and more prey than individuals in a control group. Similar to *Notechis* spp., the morphologies of individuals (specifically characteristics involved with feeding) are therefore likely explained both by hard-wired genes tailored by long-term average feeding conditions and by developmentally plastic components that allow individuals to "adjust" their phenotypes to fluctuations in prey size. Although the strength of the respective influences of developmental plasticity and adaptive traits on *B. gabonica* and *B. rhinoceros* morphology are unknown, Bonnet et al. (2001) showed that prey selection and feeding have probably been important historic factors in directing their evolutionary trajectory.

The extreme morphological adaptations of *B. gabonica*, particularly the immaculate camouflage, heavy-set appearance, and large fangs, are well documented (Luiselli 2006; Bodbijl 1994) and have made the species popular among reptile collectors and zoo herpetariums. However, despite several good dietary analyses for the species in separate parts of its range (Luiselli and Akani 2003; Perrin and Bodbijl 2001), no study or published material to date has attempted to explain the adaptive significance of the bizarre morphology of *B. gabonica* as it relates to feeding or any other part of the species life-history. This is partly because of the paucity of research attention the species has

received, but also the consequence of a practical difficulty common to all organismal studies: generating evolutionary explanations for observable traits in a species is often a speculative and difficult affair, mainly because inherently qualitative science is needed to identify and interpret selective pressures and understand how they influence the phenotypes of individuals over long timeframes. Despite this difficulty, comprehensive understanding of a species requires that its biology be scrutinized as accurately as possible through the lens of evolutionary history. For species such as *B. gabonica*, where individuals have clearly undergone strong directional selection in favour of extreme morphological traits, the adaptive significance of these traits can potentially be easier to interpret, given accurate knowledge of its ecology.

I propose that the unusual morphology of *B. gabonica* is largely the result of strong selective pressures related to diet; more specifically, pressures over evolutionary history on individuals to eat very large prey items. To test this hypothesis, I collected feeding and dietary data as part of my ecological study of *B. gabonica* within iSimangaliso. I also synthesized all known feeding records for the species across its range, including new recordings from my study of *B. gabonica* in South Africa. Using this information, *B. gabonica* diet is discussed within an ecological and evolutionary context that provides strong evidence that *B. gabonica* selectively target the largest ingestible prey within their microhabitats, and have undergone selection for morphological traits that equip individuals to do so.

Radiotelemetry allowed for extensive field observation of free-ranging snakes, and the methodology of this monitoring technique is detailed in Chapter 2. Specifically, I examined foraging behaviour, hunting strategy, diet and ecdysis among telemetered individuals. Statistical analyses were applied to data to test for trends among the foraging tendencies of individuals and for distinctions related to feeding and season. Snakes were categorized as showing “hunting behaviour” if the neck was tightly coiled and ready to strike in typical viperid ambush posture, as observed during telemetry fixes. For *B. gabonica*, this behaviour was often associated with the “spring” body positioning described in Chapter 3.

5.3 Results

5.3.1 Foraging ecology

Among telemetered Gaboon Adders, feeding activity was seasonally variable (Fig. 5.1), with individuals spending long periods of time at single localities in an ambush position, especially during summer (Table 5.1). Snakes exhibited extremely strong ambush site fidelity, often remaining immobile for periods of weeks (Chapters 3 and 4), confirming that Gaboon Adders are strict ambush predators in South Africa. On average, 70% of the sites where ambush behaviour was observed for an individual were in close proximity to (< 1 m) or partially on a game trail. These trails were usually created/used by antelope (Duiker (*Cephalophus*) and Bushbuck (*Tragelaphus*) spp.), although ungulate trails were also utilized opportunistically by a variety of smaller mammals and birds (as was evident from visual observations and the presence of spoor). I could not measure the nearness of sites to inconspicuous small mammal (e.g. rodent) runs, so it is possible that observed hunting behaviour in proximity to prey trails was higher than recorded. Similarly, I was not able to record the frequency of feeding on smaller animals because the large body size of *B. gabonica* obscures the bulge of small and even moderately-sized ingested prey. My data probably also underestimate the overall time invested in hunting by individuals because telemetry fixes were not conducted during dark hours, a suspected prime feeding time for *B. gabonica* (Bodbijl 1994).

Table 5.1 Hunting behaviour frequencies for seven telemetered *B. gabonica*: seasonal differences. Data included in the analysis were only from individuals that were monitored for a minimum of one month during each respective season. Kolmogorov-Smirnov tests were used to test for significant differences between the frequencies that *B. gabonica* exhibited hunting behaviour at non-winter and winter sites.

Snake no.	Sex	Visual observations (#)		Hunting behaviour exhibited by snakes: % of visual observations (±SD)		Exhibited hunting behaviour: *p*-values for difference testing between site types
		Non-winter sites	Winter sites	Non-winter sites	Winter sites	
1	♂	89	21	85 (36)	10 (30)	< 0.001
2	♀	42	24	64 (48)	13 (34)	< 0.001
3	♂	16	13	81 (40)	8 (28)	< 0.001
4	♂	13	23	77 (44)	17 (39)	< 0.01
5	♂	56	30	70 (46)	13 (35)	< 0.001
6	♀	55	29	56 (50)	14 (35)	< 0.005
7	♂	14	31	68 (48)	0 (0)	< 0.001

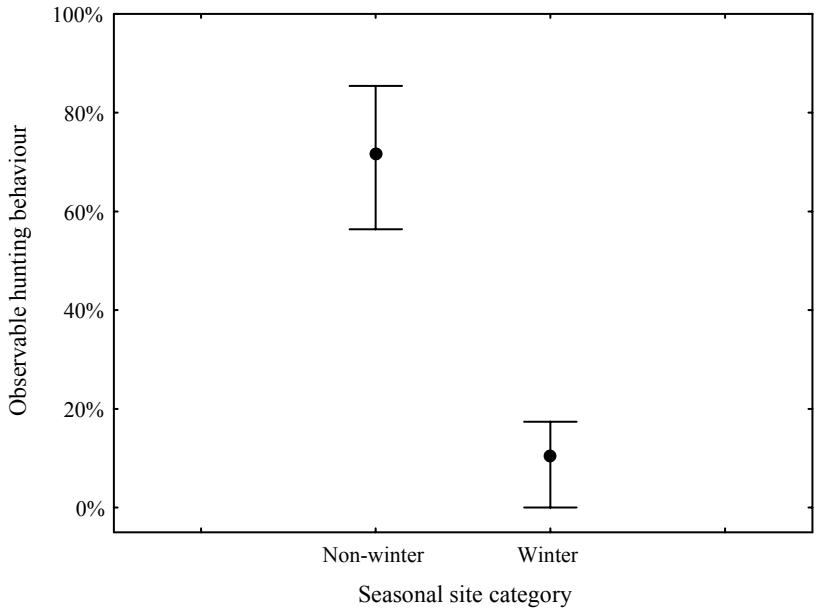


Figure 5.1 Means for the frequency of hunting behaviour observed in two seasonal categories for seven *B. gabonica*. Error bars denote max-min. Hunting behaviour among non-winter and winter sites was significantly different (Mann-Whitney U Test; $Z = 3.13$, $p = 0.0017$)

Despite heavy investments in sit-and-wait foraging behaviour by Gaboon Adders, feeding was never observed among telemetered individuals, which appeared to eat very infrequently. On six occasions, individuals were recorded to have fed on large prey (close to snake body mass), based on extremely distorted body sizes (Table 5.2; Fig. 5.2). Data collected on ecdysis supports a seasonally-biased feeding schedule for the species, with individuals eating and sloughing primarily during non-winter months. No individual monitored during this study sloughed more than twice during the active season (Table 5.2).

Using examples from two telemetred individuals, the general feeding pattern for *B. gabonica* in the iSimangaliso is illustrated as follows. On December 15th, 2006, I observed that Snake #5 (a male) was very close to shedding, based on dull body appearance and old skin covering its eyes, giving them a blue appearance. On the following fix (the 18th), the individual had clearly sloughed. From December 18th – January 23rd, the snake was observed in ambush posture during all fixes and utilized



Figure 5.2 Photographs of telemetered *B. gabonica* that had recently (≤ 48 hours previously) consumed very large prey items. Note distended scales and highly unusual body positions of individuals.



Figure 5.3 *B. gabonica* #6 with ingested Red Duiker (*Cephalophus natalensis*) from the Eastern Shores of the iSimangaliso Wetland Park

six different sites for foraging during this time period. On January 23rd I discovered the individual 25 m (linear distance) from its previous location, loosely coiled inside of a thicket containing a very large meal. The snake took until the beginning of March to digest the meal, selecting areas of dense thicket with immediately adjacent sun patches. On nine out of 12 observations during this period, the snake was loosely coiled with its head resting on top of its body. Sometime during March 1-3rd, the individual sloughed, and by March 7th, the snake had resumed hunting activity, with its body in ambush posture adjacent to a game trail.

Table 5.2 Ecdysis frequencies and predation rates on large prey for telemetered *B. gabonica*. Sloughing occurred during the active period of September-March (ANOVA; $F(1, 81) = 8.12$, $p = 0.006$).

Snake no.	Sex	Period tracked	Days tracked	No. of large meals taken	No. of sheds recorded	Month(s) ecdysis occurred
1	♂	05/12/05-23/04/07	504	1	2	Sep. 06, Mar. 07
2	♀	06/12/05-21/09/06	289	0	0	--
3	♂	15/03/06-11/07/06	114	0	0	--
4	♂	10/04/06-12/01/07	277	1	1	Oct. 06
5	♂	17/04/06-15/03/07	332	1	3	Sep. 06, Dec. 06, Mar. 07
6	♀	19/04/06-13/03/07	328	2	1	Nov. 06
7	♂	01/08/06-15/12/06	136	0	1	Nov. 06
8	♀	09/11/06-07/03/07	177	0	1	Feb. 07
9	♀	10/11/06-23/04/07	164	1	2	Jan. 07, Mar. 07
10	♂	28/03/07-25/04/07	28	0	0	--

Similarly, Snake #6 (female), was observed on January 27th, 2007 hunting with its head directly on a game trail. On January 30th, she had retreated 3 m to the inside of a thicket, having fed on a "very large" prey item. The snake appeared to be unable to coil because of the size of its meal, and its body was straight. Until March 1st the individual remained inside the same thicket digesting, head positioned on top of its body. During this time, the snake utilized sun patches within a 1 m^2 area (see

Chapter 3 for analysis of this type of behaviour). Sometime during Mar. 2-5th, the individual moved 182 m (linear distance) out of dune forest and into wooded grassland habitat, where I recorded it on March 5th hunting on another game trail. At this site, the individual killed a red duiker (*Cephalophus natalensis*) and was subsequently discovered in a nearby thicket 83 m away on March 13th (Fig. 5.3). Because the end of my field data collection was approaching, and this feeding record appeared to be particularly valuable, I removed the individual from the field and transported it to the lab, hoping to induce regurgitation and release the snake the following day. Upon arrival, I discovered that the snake had died during transport. The autopsy showed that duiker had been bitten in the lower abdomen, as this area was extremely swollen. A single fang was found tangled in the matted hair of the duiker. The duiker was 104% of the snakes' body mass. (It should be noted that other *Bitis* that have consumed large meals less than 100% of their own body mass and have died as a result (Haagner 1988), although it is likely that the stress of being picked up and transported was implicated in the Gaboon Adder's death.)

5.3.2 Diet

Prey items recorded for *B. gabonica* in the iSimangaliso during my study are among the largest recorded items to date (Table 5.3), and include a Bushbaby (*Otolemur crassicaudatus*—R. Kyle, pers. obs.), Red Duiker (*Cephalophus natalensis)*, and Banded Mongoose (*Mungos mungo*). The Red Duiker eaten by Snake #6 had the highest relative prey mass (RPM) recorded for Gaboon Vipers and is the first recording of a viperid eating an ungulate in South Africa. The largest absolute prey size record for the species is a Large-spotted Genet (*Genetta tigrina*), which weighed 2139 g and was 103% of the individual's body mass (Perrin and Bodbijl 2001).

A synthesis of *B. gabonica* feeding records confirm that, range-wide, the species specializes on mammals (Table 5.3; Fig. 5.4), although juveniles may incorporate more reptilian and avian taxa in their diets (Luiselli and Akani 2003; Perrin and Bodbijl 2001; this study). During my study, I recorded the feathers of an unidentified bird in the faeces of a male neonate that was found in the same thicket as a telemetered individual. A sub-adult male from a residential garden in St. Lucia village was collected after the owner of the property observed the individual eating a Natal Robin (*Cossypha natalensis*). Additionally, a large female captured outside protected area in the Dukuduku

squatter camp was purported to be preying on adult chickens at the fringe of a settlement; faecal material collected from this individual verified this claim.

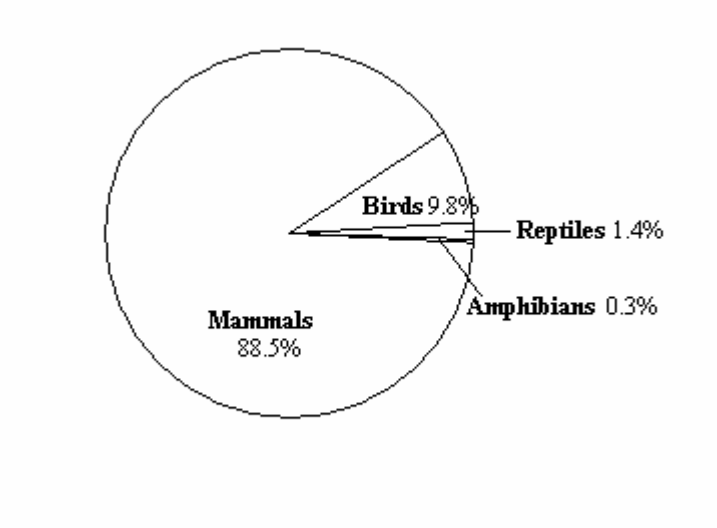


Figure 5.4 Prey taxa representation for all *B. gabonica* feeding records (n = 347)

Table 5.3 Inventory of all prey records for *B. gabonica* across its range, including anecdotal accounts from published literature. CM = Cameroon, DRC = Democratic Republic of Congo, NG = Nigeria, TZ = Tanzania, UG = Uganda, SA = South Africa, ZA = Zambia, ZM = Zimbabwe.

Biological Name	Common Name	*n*	Country	Reference
Mammals				
Aethomys chrysophilus	Red Veld Rat	19	SA	Perrin and Bodbijl 2001
Aethomys spp.	Veld Rat spp.	4	ZA	Perrin and Bodbijl 2001
		1	ZM	Perrin and Bodbijl 2001
Arvicanthis niloticus	African Grass Rat	1	UG	Pitman 1974
Atherurus africanus	African Brush-tailed Porcupine	1	CM	Stucki-Stirn 1979
Bdeogale crassicauda	Bushy-tailed Mongoose	1	MZ	Peters 1882
Cephalophus natalensis	Red Duiker	1	SA	This study
Cephalophus sp.	Duiker sp.	1	CM	Stucki-Stirn 1979
Chlorocebus spp.	Monkey spp.	1	ZM	Spawls and Branch 1997
Cricetomys gambianus	African Giant Pouch Rat	75	NG	Luiselli and Akani 2003
		1	ZM	Perrin and Bodbijl 2001
		1	UG	Pitman 1974
Dasymys incomtus	African Water Rat	1	DRC	Schmidt 1923
Felis catus	Domestic Cat	1	UG	This study
Funisciurus sp.	Striped Squirrel sp.	5	NG	Luiselli and Akani 2003
Genetta sp.	Genet sp.	1	UG	Pitman 1974
Genetta tigrina	Cape Genet	1	SA	Perrin and Bodbijl 2001
Gerbilliscus leucogaster	Bushveld Gerbil	1	TZ	Ionides and Pitman 1965
Grammomys dolichurus	Woodland Thicket Rat	8	SA	Perrin and Bodbijl 2001
		1	ZM	Perrin and Bodbijl 2001

Helioscurus sp.	Sun Squirrel sp.	1	NG	Luiselli and Akani 2003
Lemniscomys striatus	Typical Striped Grass Mouse	63	NG	Luiselli and Akani 2003, Angelici et al. 2000
Lophuromys flavopunctatus	Yellow-spotted Brush-furred Rat	1	TZ	Barbour and Loveridge 1928
Mastomys natalensis	Natal Multimammate Mouse	4	SA	Perrin and Bodbijl 2001
		1	ZM	Perrin and Bodbijl 2001
Mastomys sp.	Multimammate Mouse sp.	1	UG	Pitman 1974
		1	TZ	Loveridge 1942
Mungos mungo	Banded Mongoose	1	SA	This study
Mus minutoides	African Pygmy Mouse	2	SA	Perrin and Bodbijl 2001
		1	UG	Pitman 1974
Mystromys albicaudatus	White-tailed Rat	1	SA	Perrin and Bodbijl 2001
Otolemur crassicaudatus	Brown Greater Galago	1	SA	This study
Otomys irroratus	Common Vlei Rat	1	ZM	Perrin and Bodbijl 2001
Otomys spp.	Vlei Rat spp.	36	SA	Perrin and Bodbijl 2001, This study
Paraxerus vexillarius	Svynnerton's Bush Squirrel	1	TZ	Barbour and Loveridge 1928
Petrodromus tetradactylus	Four-toed Elephant Shrew	1	SA	Perrin and Bodbijl 2001
Rattus rattus	House Rat	2	NG	Luiselli and Akani 2003
Rattus spp.	Rat spp.	2	UG	Loveridge 1942, Pitman 1974
		1	TZ	Barbour and Loveridge 1928
Rhynchocyon cirnei	Checkered Elephant Shrew	1	TZ	Pitman 1974
Suncus spp.	Shrew spp.	12	NG	Luiselli and Akani 2003
		2	SA	Perrin and Bodbijl 2001
Thallomys paedulcus	Acacia Rat	4	SA	Perrin and Bodbijl 2001
Thryonomys sp.	Cane Rat sp.	1	UG	Pitman 1974
Unidentified Muridae spp.		35	NG	Luiselli and Akani 2003, Angelici et al. 2000
		4	SA	Haagner 1986, Perrin and Bodbijl 2001, This study
Birds				
Caprimulgus sp.	Nightjar sp.	1	SA	Perrin and Bodbijl 2001
Chlorocichla flaviventris	Yellow-bellied Greenbul	1	SA	Perrin and Bodbijl 2001
Cossypha henglini	Heuglin's Robin	1	SA	Haagner 1986
Cossypha natalensis	Natal Robin	6	SA	Perrin and Bodbijl 2001, Haagner 1986, This study
Erythropygia signata	Brown Scrub Robin	1	SA	Perrin and Bodbijl 2001
Gallus gallus	Domestic Chicken	1	SA	This study
		1	NG	Cansdale 1948
Rallidae	Rail sp.	1	DRC	Schmidt 1923
Sarothrura elegans	Buff-spotted Flufftail	1	SA	Perrin and Bodbijl 2001
Turdidae sp.	Thrush sp.	1	TZ	Ionides and Pitman 1965
Unidentified Aves spp.		11	SA	Perrin and Bodbijl 2001, This study
		5	NG	Luiselli and Akani 2003
		2	ZA	Perrin and Bodbijl 2001
		1	ZM	Perrin and Bodbijl 2001
Reptiles				
Mochlus fernandii	True Fire Skink	2	NG	Luiselli and Akani 2003
Trachylepis sp.	Skink sp.	3	NG	Luiselli and Akani 2003
Amphibians				
Trychobatrachus robustus	Hairy Frog	1	NG	Luiselli and Akani 2003

5.4 Discussion

5.4.1 The "large-prey hypothesis": ecological support

Fix observations and new feeding records of telemetered *B. gabonica* inside the iSimangaliso revealed two trends: individuals select game trails (= paths through suitable *B. gabonica* habitat usually created by ungulates but also utilized by other taxa) as sites for ambushing prey, and individuals ate large meals that made use of such trails. However, with few exceptions, prey records (Table 5.3) show that *B. gabonica* feeds primarily on small mammals (various rat and mice species) across its range. This would seemingly contradict my hypothesis that Gaboon Adders selectively target large prey items that weigh close to their own body mass, and the general foraging trend observed for *B. gabonica* in the iSimangaliso.

I suggest that the compilation of historical feeding records for the species is biased and misleading with regards to *B. gabonica* preferred diet, because the localities of the majority of the dietary records are from areas that have undergone significant habitat transformation and depletion of larger prey species. This includes the two major diet studies on the species (Luiselli and Akani 2003 and Perrin and Bodbijl 2003) of which most of the records (87.4%) found in Table 5.3 are from – studies of *B. gabonica* in habitats that were unprotected and significantly altered/disturbed by human activity, especially the study of Perrin and Bodbijl (2003). At the study sites of Luiselli and Akani (Nigeria) and Bodbijl (South Africa), *B. gabonica* habitat was fragmented and interspersed with farmlands and plantations, and widespread informal settlements, respectively. In both areas, larger animals that were once prevalent and suitable prey for *B. gabonica* (e.g., small antelope (*Cephalophus* spp.), monkeys (*Chlorocebus* spp.), bushbabies (*Otolemur* spp.), genets (*Genetta* spp.), mongooses (family Herpestidae)) had either been eradicated or were extremely scarce (due to hunting, poaching, and displacement), and are thus not truly represented in the feeding records. With one exception (a Large-spotted Genet; Perrin and Bodbijl 2001), all of the feeding records from Perrin and Bodbijl (2001) and Luiselli and Akani (2003) consist of rodents and birds.

Does the "large prey" hypothesis therefore no longer apply to *B. gabonica* in areas of sub-optimal habitat where prey that is close in size/mass to individual snakes is non-existent? In practice yes, but

the trend of feeding on large meals is still evident. In marginalized habitats where suitable ambush trails and large prey are scarce, *B. gabonica* still appear to consume the largest prey available: the gut content analyses of Perrin and Bodbijl (2001) and Luiselli and Akani (2003) both show that adult individuals selectively fed on the largest rodent species present within their microhabitats (*Cricetomys gambianus* and *Lemniscomys striatus* in Nigeria, and *Otomys* spp. and *Aethomys chrysophilus* in South Africa). However, such "large" meals are still relatively small compared to prey options (taxa larger than rodents) available in protected areas; the assumed "preferred" diet of *B. gabonica* has been extrapolated from research on individuals that fed exclusively on rodents because only rodents were available in their habitat, but diet under optimal ecological conditions is biased towards larger taxa (as supported by hunting behaviour and diet records of individuals from my study within protected area).

Although research suggests that Gaboon Adders target large prey (high RPM), this hypothesis requires further investigation in protected areas at various locations within *B. gabonica* range in order to be validated. In West Africa, the Sooty Mangabey (*Cercocebus torquatus atys*), a terrestrial, forest-dwelling monkey species, employs a warning vocalization for *B. rhinoceros* (sister species to *B. gabonica*) similar to that for other predators—but not for other snakes, presumably because other forest taxa (e.g. Forest Cobras, *Naja melanoleuca*) ignore Mangabeys due to gape limitation (Range and Fischer 2004). As the diet of *B. gabonica* in unprotected areas consists primarily of rodent taxa, a starting point for future research should be investigating whether individuals in areas such as Dukuduku must make greater foraging investments (e.g., increased levels of hunting and feeding) to compensate for the scarcity or unavailability of larger prey (e.g. antelope). Anecdotal evidence and feeding records from my study suggest that individuals will consume domesticated animals (e.g., feral cats and chickens) in the absence of suitably-sized indigenous fauna, although the frequency of such predation is unknown.

Among snake taxa, larger individuals and species generally kill proportionately larger prey items (Greene 1997). This selective feeding strategy has proven nutritional and energetic benefits, and reduces the risks associated with hunting and restraining prey (Rodgriguez-Robles 1999; Shine and Thomas 2005), although killing and consuming large meals can also engender risk (Haagner 1988). While it is normally advantageous for snakes to target big meals, "large" prey for a species may

differ among sex, age group, location, and season. Intraspecific dietary differences are not uncommon, with ontogenetic shifts in dietary composition the normal pattern (Greene 1997). For some taxa, this necessitates, for example, a shift from smaller reptilian to larger mammalian prey (Shine et al. 2006b), or from nestling rodents to adult rodents (Luiselli and Akani 2003) as gape and body size increases. As the largest Old World viperid, in terms of both length and girth (Mallow et al. 2003), it should come as no surprise — according to optimal foraging theory and the widespread feeding trend among snakes (Arnold 1993) — that *B. gabonica* targets larger meals relative to other smaller *Bitis*. However, I suggest that under suitable conditions, individuals not only selectively feed on large prey but also have a higher average RPM per meal compared with most other species; due to their extreme morphology and ecology, Gaboon Adders are able to eat prey items closer to their own body mass and it benefits them biologically to do so.

5.4.2 The "large-prey hypothesis": morphological support

As a strict ambush forager, *B. gabonica*, like many other viperids, are not as mobile and do not feed as frequently or successfully as active foragers. However, among reptiles, *B. gabonica* are perhaps the most extreme sit-and-wait predators; individuals, aided by highly camouflaged bodies, frequently remain immobile at hunting sites for periods of weeks (see previous chapters). A high level of crypsis, though necessary for extended periods of ambush foraging, is not necessarily an adaptation directly related to feeding. The first, and perhaps most important, adaptation that *B. gabonica* has adapted for large prey is a large head. For gape-limited predators like snakes, that cannot chew their food, a large head is a necessity for consuming large prey and a large, triangular-shaped head is a diagnostic characteristic of many viperid taxa. The head of *B. gabonica* is particularly striking because of its disproportionate size relative to its body; the average head width/body length ratio for *B. gabonica* is probably the largest of any snake in the world (Mallow et al. 2003). It is not unreasonable, therefore, to predict that the species should have a higher average RPM compared with most other taxa, due to the relative large size and structure of the feeding anatomy. Additionally, a large, wide head possibly facilitated the evolution of other *B. gabonica* feeding adaptations, such as exceptionally wide movement of the eyes (suspected to maximize peripheral vision for feeding; Parry 1975) and long fangs (Merhtens 1987).



Figure 5.5 A telemetered *B. gabonica* in ambush posture adjacent to an antelope trail in dune forest habitat

Encased within the giant heads of *B. gabonica* (and sister species *B. rhinoceros*) are a set of massive solenoglyphous fangs up to 40 mm in length; fangs much larger than those of any other species in the world (Mehrtens 1987). Bonnet (et al. 2001) suggests that the extreme size of *B. gabonica* fangs is evidence that strong selection was involved in their evolution; discriminatory pressures on fang size that are not as influential in the evolutionary history of other taxa. However, the adaptive significance of having giant fangs is unknown. Under my "large-prey" hypothesis, I suggest that the long fangs of *B. gabonica* have evolved to accommodate feeding on large prey, because long fangs are needed to penetrate and envenomate the thick body tissue of bigger animals. Additionally, such prey must be killed quickly if an individual is to recover its meal without expending energy in extended movement and abnormal exposure to predation risk. This is achieved by delivering copious

venom yields delivered after a strike: Marsh and Whaler (1984) report a maximum wet yield of 9.7 ml for *B. gabonica*, by far the largest of any snake in the world.

Similar to some other snake species, *B. gabonica* probably inject increasing amounts of venom with increasing prey size, which could explain the strong selective pressure on the species for the large venom glands and delivery quantities that are needed to effectively kill big prey (Marsh and Whaler 1984). (Another function of snake venom is as a digestive aid [Greene 1997], so large injection quantities may also help *B. gabonica* digest larger animals faster after ingestion.) My data, although few, show that meals approximate to snake body mass were indeed killed quickly: in all instances, individuals moved < 100 m between the ambush site and the post-feeding locality the snake was observed at. However, I was unable to determine the success rate for individuals successfully killing and recovering large prey (*n* animals targeted / *n* animals consumed), although similar studies on ambush-foraging viperids suggest individuals exhibit a relatively high frequency of missed strikes (Clark 2006; Shine et al. 2002).

Bitis gabonica use their fangs to manipulate prey towards the esophagus while eating (Bonnet et al. 2001; pers. obs.). To execute this "pterygoid walk" on large prey, the big, robust fangs and strong maxillary bones provide an advantage when feeding. However, the feeding biology of *B. gabonica* also reveals a greater advantage that enormous fangs afford individuals: unlike most other taxa, individuals frequently retain their grip on smaller prey after the strike instead of releasing the meal and subsequently using visual or chemosensory cues to track down an animal after it succumbs to envenomation (Bodbijl 1994; Bonnet et al. 2001; pers. obs.). This adaptation may be beneficial for feeding on very large prey and maintaining an extremely sedentary foraging strategy, because individuals can opportunistically supplement their diet with smaller animals without have to expend energy in scent-trailing. Hunting in close proximity to game trails facilitates this, as these trails are the most likely place to encounter large prey while simultaneously having access to smaller, opportunistic meals (Fig. 5.5). Additionally, premium hunting sites are not compromised by having to track down prey (and thus spread their scent) in order to find prey that has been killed as a short-term substitute for a larger meal. *Bitis gabonica* can therefore opportunistically feed on smaller animals when available, and not give up foraging position, until an optimal large meal is captured.

Clark (2002) also found that large *Crotalus horridus* selectively targeted larger prey species, but that they did not exclude smaller prey items from their diets. Reasons for this feeding strategy are unclear, as some snakes exclude smaller prey in their diet as body size increases (Arnold 1993). However, research has shown that although ambush foraging snakes pay a high metabolic cost to digest prey (they have a high specific dynamic action), the energy cost to digest small and large prey items makes up a similar proportion of the energy content of the meal (Secor and Diamond 1997; Cruz-Neto et al. 1999; Clark 2004). Since the energetic cost of consuming large and small prey is similar, killing large prey is therefore a more profitable investment for a snake because of the comparable greater energy provided by a bigger meal. Under sub-optimal conditions though, when individuals cannot capture larger prey items, predation on smaller animals is better than no meal at all (Clark 2004).

The behaviour of *B. gabonica* to selectively feed on large prey items explains why individuals may spend extremely long periods at single ambush sites without moving: because the only movements involved with feeding, a defining aspect of any species' ecology, are the selection of suitable foraging locations (rare judging from the low number of movements of individuals between sites; Chap. 3) and the retrieval of large prey once it has been envenomated (also uncommon; Table 1). This two-stage prey finding strategy is common among viperids (Clark 2006; Reinert 1984), but because *B. gabonica* are able to hold on to smaller prey after the strike, individuals essentially remove the second stage of movement because they can kill and consume these smaller items without moving from the ambush site. For larger prey items (e.g. *Cephalophus* sp.), energy costs associated with movement are required to scent-trail envenomated meals, but the long-term energy gains make these movements worthwhile. Therefore, *B. gabonica* that feed on large prey facilitate the high levels of immobility characteristic of individuals (see Chapter 3).

Feeding records from my study and others show that *B. gabonica* can consume prey items more than 100% of their own body mass, meaning individuals are capable of consuming in one meal the energy budget some biologically similar viperids consume annually under certain conditions (Beaupre 1996; Clark 2002). While difficult to show empirically, I would hypothesize that a correlation exists between the time spent at an ambush site and meal size for species with a sit-and-wait strategy. Evidence from other studies indicates that the more often an ambush foraging snake feeds, the more

it moves (Clark 2006; S. Beaupre, pers. comm.). *Bitis gabonica* appears to have reduced feeding related movement on an ecological level by not letting go of small prey after the strike and selectively targeting large meals (therefore reducing the number of required meals). On an evolutionary level, the species has acquired adaptations that allow individuals to consume large meals, such as large fangs and a disproportionately large head and body.

5.5 Conclusions

Relative large heads, body sizes, fangs and venom yields are homologous characteristics among the large *Bitis* (Fig. 5.6), and are exhibited to an extreme degree in the *B. gabonica/rhinoceros* clade; a phenomenon that I hypothesize is the result of strong directional selection on individuals to specialize on very large prey. I have presented the ecological evidence for this theory, showing how the unique morphological traits of *B. gabonica* allow individuals to eat large meals and facilitate what is one of the most extreme sit-and-wait foraging strategies currently observed among the viperids.

What ecological circumstances produced the bizarre phenotype of *B. gabonica*, however, requires further research. It is possible that the low densities of small mammals in African forests (Bodbijl 1994) and/or interspecific competition with other snakes (Luiselli 2006) played important roles, forcing body size shifts due to strong selection imposed by the size of available prey items (see Keogh et al. 2005). Competition for food is much stronger in tropical snake communities, and many tropical snakes must partition the food resource (prey type and/or size; Luiselli 2006a). However, when this resource cannot be partitioned among taxa, competitive exclusion can occur (Luiselli 2006a). This may have been the case historically for *B. gabonica*, with selective pressure to specialize on large prey (animals other snake taxa could not hunt or consume) paving the way for the "extreme" morphology and "slow" ecology exhibited by the species.

Data from telemetred *B. gabonica* within iSimangaliso show that this protected area provides individuals a more heterogeneous prey assemblage and greater abundance of game trails for hunting than do adjacent, unprotected areas. While Gaboon Adders are able to feed on large prey within the iSimangaliso, it is unclear how similar *B. gabonica* feeding frequencies are in protected and unprotected areas and to what degree human disturbance in unprotected areas impacts the foraging



Bitis nasicornis



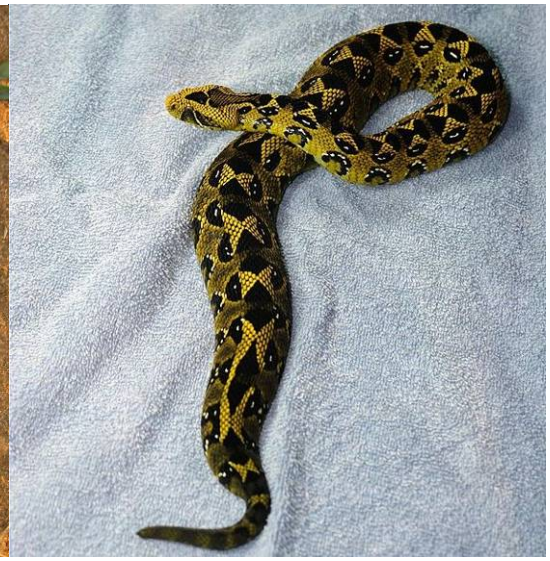
Bitis rhinoceros



Bitis gabonica



Bitis arietans



Bitis parviocula

Figure 5.6 Morphological similarities between the giant *Bitis* of Africa. All are terrestrial ambush foragers with extremely long fangs (relative to other taxa), stout-bodies, and adult lengths that approach or exceed 1m. Note resemblances among species in regards to general body and head shape, geometric dorsal patterning, and "tear-drop" striping between the eye and labial scales.

strategy and success of individuals. Additionally, given recent studies that support the influence of adaptive developmental plasticity among snake taxa (Aubret and Shine 2007; Aubret et al. 2004; Bonnet et al. 2001), even on the morphology exhibited by individuals in a population over a relatively short time period (Keogh et al. 2005), the elimination of certain *B. gabonica* prey items (e.g. larger taxa) due to increasing alteration of *B. gabonica* habitat by humans across the species' range could have a direct effect on both the morphology and ecology of the species.

If *B. gabonica* populations are no longer exposed to large prey, as is the scenario now in several unprotected/disturbed areas, gene mutations accumulated by individuals over evolutionary history that code for large head and body sizes may be lost in subsequent generations. Moreover, the potential ecological ramifications of repeated exposure to only small prey could be negative for the species due to forced competition with other taxa, as already suggested for *B. gabonica* and *B. nasicornis* in an unprotected area in West Africa (Luiselli 2006b). Long term studies of *B. gabonica* populations inside and outside of protected areas in Africa are needed to determine the impact of prey availability and selection on the species' ecology and morphology.

Chapter 6: Conclusions, conservation implications and grounds for future study

6.1 *Bitis gabonica* ecology: a synopsis of findings from Chapters 1-5

Bitis gabonica is a sedentary species well-known for its docility, striking geometric patterning, large body size and potent venom. Morphologically and ecologically well-adapted for life on the forest floor, *B. gabonica* is inactive for much of the time, but is nonetheless capable of moving long distances and occupying large home range areas. Movements vary among individuals, but distinct patterns are evident in the spatial ecology of the species. A definitive bi-modal seasonal activity pattern exists for *B. gabonica* in subtropical South Africa. There are movement peaks in spring and fall with highly sedentary periods in winter, and to a lesser extent in late summer. The remarkable capacity to remain motionless (while not brumating) for months at a time during cooler weather makes South African *B. gabonica* ecologically unique compared to other snakes, including *B. gabonica* populations of tropical affinity.

Home range estimations calculated using two methods (minimum convex polygons and kernel density contours) show that male *B. gabonica* can occupy home range areas exceeding 40 ha, while female home ranges are closer to 10 ha. Core areas of activity (areas individuals use most within a home range) are approximately 7 ha, with males generally having larger core activity areas than females. Movement frequency (site relocation) for individuals is low, and typical movement behaviour outside of the mating season consists of occasional small movements (< 15 m), followed by a longer, continuous move (> 50 m), usually related to hunting. During the mating season (March-May) activity increases, and individuals can move over 500 m in 24 hours.

Bitis gabonica habitat preferences are strongly influenced by season, with individuals selecting open-canopied areas (forest edge, grassland, secondary grassland and open woodland) during cold periods, presumably because closed-canopy habitat (e.g. coastal dune forest) is not adequate for the species' thermoregulatory requirements during winter. However, microhabitat features (with the exception of overhead canopy cover) are structurally similar among sites selected in both winter and non-winter months. These sites are generally adjacent to or inside mature thickets – dense shrubbery in the

understory under which little or no vegetation grows (e.g. *Isoglossa woodi* thickets). Thickets are a critical habitat feature for *B. gabonica* suitable habitat because of the feeding, thermoregulatory and protective advantages they provide relative to other structural features within preferred macrohabitat.

Bitis gabonica generally do not feed during winter, but individuals spend extended periods of time waiting in ambush for prey during warmer months. Individuals exhibit strong ambush site fidelity, and often remain motionless for weeks at a single hunting location until prey is killed. *B. gabonica* frequently hunt in close proximity (< 1 m) to game trails created by antelope, and are capable of killing and consuming prey > 100% of individual body mass (e.g. Red Duiker; *Cephalophus natalensis*). Protected areas like iSimangaliso provide *B. gabonica* a more heterogeneous prey assemblage and greater abundance of game trails for hunting than do adjacent, unprotected areas. Although *B. gabonica* likely target the largest prey items available, individuals may opportunistically kill smaller animals under some circumstances.

Adult *B. gabonica* have very few natural predators. Extreme crypsis coupled with adaptive behaviours such as burrowing in leaf litter and high tolerance to various forms of disturbance enable *B. gabonica* to remain immobile for long periods of time. These traits illustrate how evolutionary pressures can develop species with "slow" yet successful life-history strategies.

6.2 Conservation implications

Conservation and management, threats to *B. gabonica*, and issues concerning the snake-human interface are detailed in the Addendum. However, two topics related to *B. gabonica* conservation biology are specifically discussed in this chapter because of their importance in describing the conservation status of the species in South Africa

6.2.1 Lack of genetic variation aross the range of B. gabonica

Until recently, *B. gabonica* was considered an infraspecific clade composed of two subspecies: the Central African Gaboon Adder (*Bitis gabonica gabonica*), and the West African Gaboon Adder (*Bitis gabonica rhinoceros*). The molecular study of Lenk et al. (1999) proposed that the subspecies

should be raised to specific status (*Bitis gabonica* and *Bitis rhinoceros*), and this taxonomic delineation is currently accepted among researchers (Fig. 6.1). Nonetheless, the *Bitis* phylogeny cannot be considered fully resolved until comprehensive geographical molecular sampling is undertaken for all taxa within the genus, especially for species' with patchy distributions.

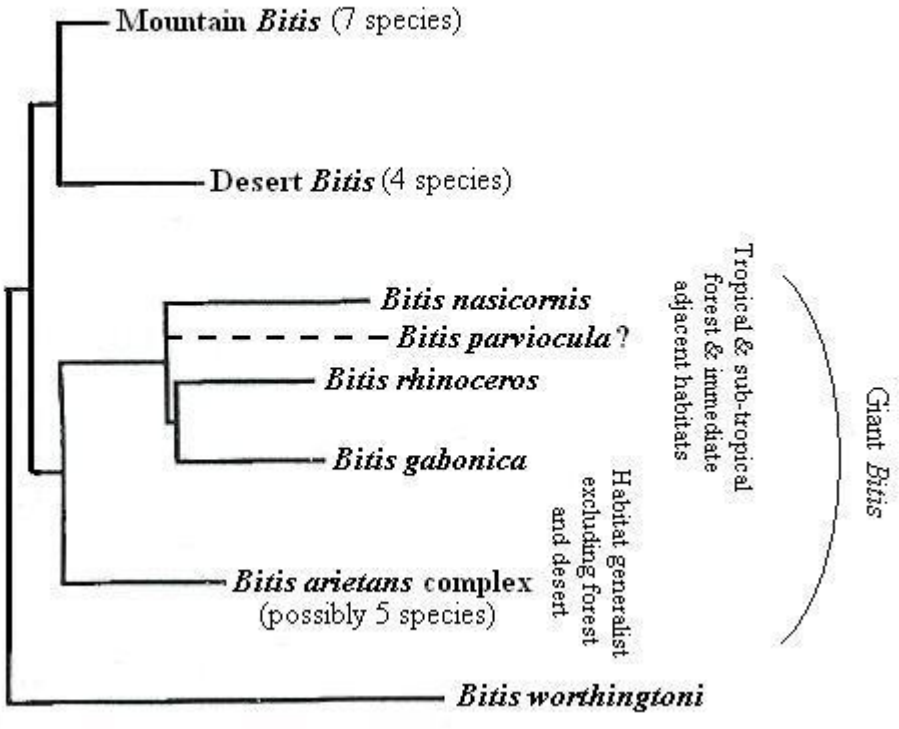


Figure 6.1 Phylogram of known *Bitis* (derived from mitochondrial DNA sequence analysis by Lenk et al. [1999] and updated to incorporate recent findings) depicting the genus partitioned into five monophyletic clades. The "mountain" *Bitis* clade (*B. albanica, B. armata, B. atropos, B. cornuta, B. inornata, B. rubida* and *B. xeropaga*) consists primarily of rock-dwelling species, although the exact placement of *B. albanica, B. armata, B. inornata,* and *B. rubida* within the group awaits genetic analyses. Likewise, the positioning of *B. heraldica* (found in central Angola) among the other members of the "desert" clade (*B. caudalis*, *B. peringueyi* and *B. schneideri*) is unknown, but the species is closest morphologically to *B. caudalis*. I tentatively placed *Bitis parviocula* (known from under ten specimens collected in southwestern Ethiopia) within the *gabonica* clade based on morphological affinities to other group members, according to Groombridge (1980). The *B. arietans* clade, currently under molecular scrutinization (W. Wuster pers. comm.), according to Lenk et al. (1999) is not as close genetically to the *gabonica* clade as the two Dwarf Adder clades are to each other, despite recorded hybridization between *B. gabonica* and *B. arietans* in southern Africa (Branch 1998). *Bitis worthingtoni*, a small species found in high altitudes of the Kenyan Rift Valley, represents the genus' monotypic basal clade.

Bitis arietans, although morphologically similar to *B. gabonica*, is more widespread in Africa and is ecologically adapted to a wider range of biomes. Recent molecular data show that *B. arietans* does not represent a single species but is a clade consisting of potentially five species (W. Wuster, unpubl. data). Although there is no evidence that *B. gabonica* exhibits considerable intraspecific phenotypic variation across its range, it has been hypothesized by several researchers that because of the species patchy distribution (Fig. 6.2), *B. gabonica* may actually constitute several species, similar to *B. arietans*.



Figure 6.2 *Bitis gabonica* distribution in sub-Saharan Africa. Note isolated populations in Kenya, eastern Zimbabwe/ northern Mozambique and South Africa.

Since determining the genetic uniqueness of South African *B. gabonica* is necessary for evaluating the conservation status of the population, I outsourced tissue from eight Zululand *B. gabonica* for molecular analysis. Cytochrome b sequences of these South African *B. gabonica* differed from a Cameroonian specimen by 0.35%, or a total of only 2 base pair substitutions out of 597 bp. Zululand *B. gabonica*, together with the Cameroonian sample, differed by approximately 2 % (~ 12 substitutions) from a GenBank sequence of a *B. gabonica* from the Congo. However, nearly all of the additional differences occurred in the last 100 bp of the Congo sequence; meaning that these differences are most likely due to reading errors in the Congo sequence, and should be discarded (W. Wuster unpubl. data).

A remarkable, unexpected degree of genetic homogeneity was found across the wide, discontinuous distribution of *B. gabonica*. This finding was also surprising because *B. gabonica* is restrained to tropical and subtropical forest, and theoretically should not be able to easily disperse over long distances and establish new populations because of its extraordinarily sedentary disposition. The upshot is that South African *B. gabonica* are genetically similar to conspecific populations throughout sub-Saharan Africa, which means that from a molecular standpoint, the *B. gabonica* conservation status in South Africa is more stable than what was previously assumed.

6.2.2 Bitis gabonica habitat protection and availability

Because the distribution of *B. gabonica* is very restricted in South Africa, the major conservation concern for the viability of the species in recent years has been the fragility of remaining suitable habitat given the rapid increase of human activity (namely deforestation and tree-felling for fuel and living structures by thousands of impoverished settlers) in coastal Zululand (Bodbijl 1994). Previous research of *B. gabonica* in South Africa took place in the 2500 ha Dukuduku Forest; pristine coastal lowland forest that has been systematically destroyed by illegal squatters over the past 20 years (Lawes et al. 2004). Because this unprotected area was generally regarded as harbouring the densest population of *B. gabonica* in the country, panic for the species' survival in South Africa reached a crescendo in the mid-1990s, when the remaining population was estimated to consist of no more than 500 individuals (Bodbijl). Approximately 200 individuals were translocated from Dukuduku to Umlalazi Nature Reserve until the controversial operation was halted by Ezemvelo KZN Wildlife ecologists.

One of the aims of my study was to look at *B. gabonica* habitat use in protected area (iSimangaliso Wetland Park). My data show that *B. gabonica* utilize a wider range of habitats than was previously assumed (see Chapter 4) and that there is no evidence that *B. gabonica* occur at levels below normal within iSimangaliso. Although the destruction of Dukuduku was harmful to the species, *B. gabonica* are certainly not exclusively confined to the Dukuduku area (Fig. 6.3), meaning earlier translocation efforts were probably unnecessary. Translocation can be beneficial for some threatened species, but only if the benefits outweigh the risks (Dodd and Seigel 1991; King et al. 2004; relocation of *B. gabonica* is discussed in detail in the Appendix).

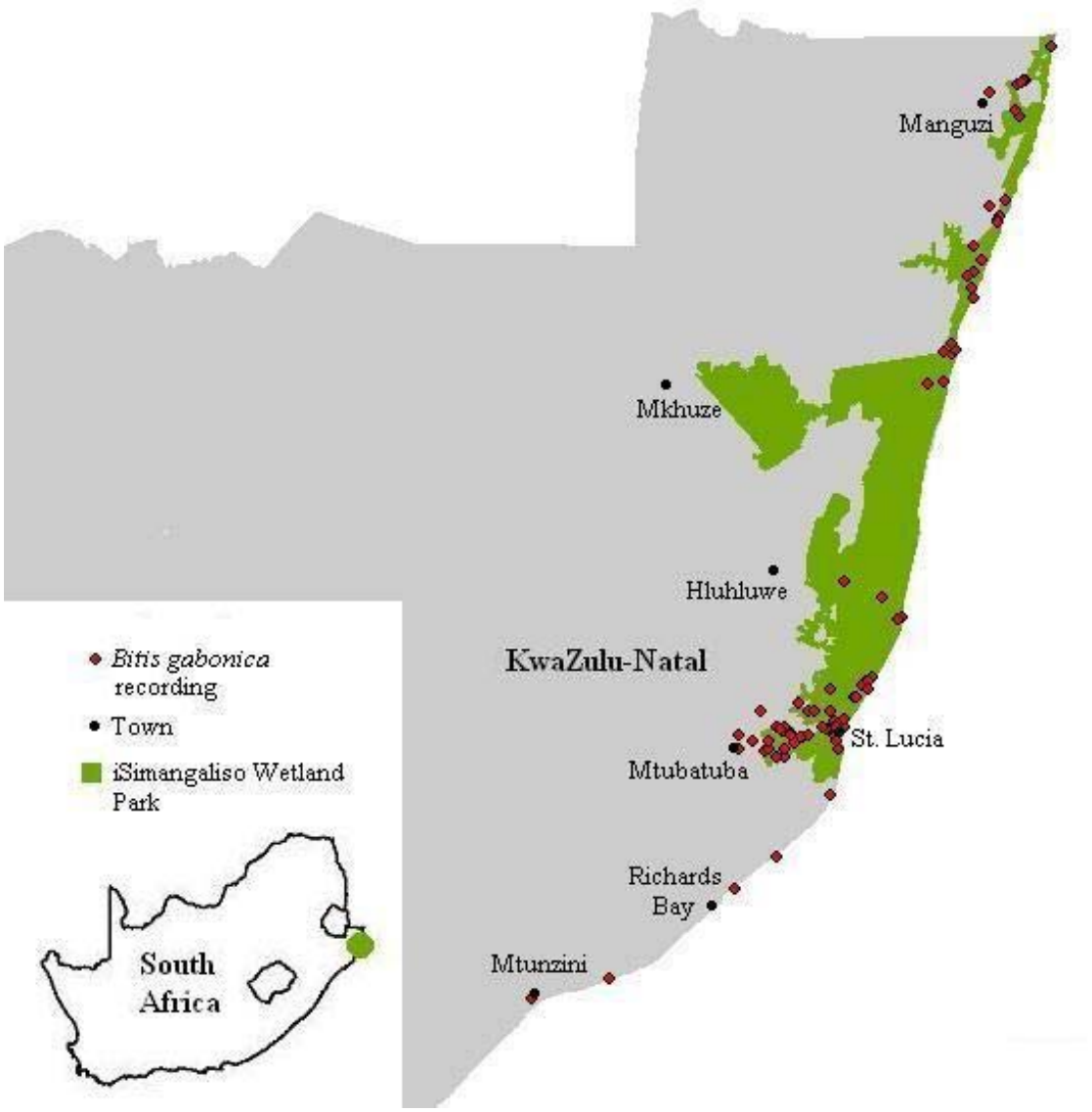


Figure 6.3. Importance of iSimangaliso Wetland Park to the South African *B. gabonica* population as inferred from verified recordings (n = 101) of the species

Historically, much subtropical forest in the country was destroyed for the cultivation of sugarcane and *Pinus* and *Eucalyptus* plantations (Lawes 2002; Armstrong 2002), and today unprotected coastal forests remain under threat from strip-mining, land invasion and land transformation by humans (Mucina and Rutherford 2006). Although the Northern Coastal Forest bioregion is relatively small (467.05 km^2), it is listed as "well-protected " by the South African National Biodiversity Institute

(SANBI), primarily because a large proportion of this vegetation type is harbored by the iSimangaliso Wetland Park (Mucina and Rutherford 2006). The vast majority of *B. gabonica* recordings are also inside or immediately adjacent to iSimangaliso (Fig. 6.3, Chapter 4), attesting to the importance of this Park both for *B. gabonica* suitable habitat and the South African *B. gabonica* population. Continued protection of the iSimangaliso coastal dune forest corridor is paramount to the long-term viability of the species in Zululand.

Bitis gabonica is not alone in its dependence on iSimangaliso: sixteen species of reptiles that occur within the park's boundaries are listed in CITES appendices (Schedule 14), five species of frogs found in the Park are endemic to KwaZulu-Natal, and several species of reptiles (*Prosymna janii*, *Scelotes vestigifer, S. fitzsimonsi, Bradypodion setaroi*) are found exclusively in the coastal dune system that is protected by iSimangaliso (Broadley 1990, KZNNCS 1998).

6.3 Further research

Although *B. gabonica* has received significant research attention in comparison with other African snakes, many facets of the species' biology await future study. The most obvious gap in the current ecological knowledge of *B. gabonica* is an understanding of population densities in South Africa. Density estimation is difficult not only because of the species' cryptic morphology and sedentary behaviour, but also because subtropical forest is very heterogeneous (Van Aarde et al. 1996), and *B. gabonica* preferred microhabitats are variable within these areas (Chapter 4).

Luiselli (2006c) calculated a density of 0.157 ± 0.22 individuals ha -1 for *B. gabonica* in Nigeria. Using data from my study of a resident male (Snake #1, tracked 504 days), whose 95% KD home range estimate (47.20 ha, see Chapter 3) eclipsed that of a resident female (Snake #9, tracked 164 days), and assuming other *B. gabonica* did not share the same area, an estimate of 1900 individuals (50% male, 50% female) is calculated for the total South Africa population based on approximate available macrohabitat (450 km^2, Mucina and Rutherford 2006). This estimate is likely too conservative because it assumes complete competitive exclusion for habitat between the sexes, and supposes all coastal forest is suitable habitat for *B. gabonica*.

Using the 50% KD home range estimates ("core areas" of use, see Chapter 3) of the same two telemetred *B. gabonica* in the equation, the total population estimate increases to approximately 3500 individuals. Assuming Luiselli's (2006c) estimate of 0.157 ± 0.22 individuals ha −1 holds for Zululand *B. gabonica*, the estimate rises to over 28000 individuals. This number may be too high because even though *B. gabonica* is sympatric with *B. nasicornis* in West Africa (which may influence local densities due to resource partitioning among the species; Luiselli 2006c), South African *B. gabonica* densities are presumed to be lower than other populations (Isemonger 1968) and are encountered less frequently in suitable habitat (this study; Luiselli 2006c). A study similar to that of Luiselli (2006c) is needed in South Africa to accurately estimate *B. gabonica* density.

Further research on the frequency of mating and the length of gestational periods for *B. gabonica* in South Africa is needed, as it appears reproductive biology, like some aspects of the species' ecology (see Chapter 3), may differ from other *B. gabonica* populations. It is probable that gestation is longer than 12 months in South Africa. Neonates measure between 240 and 370 mm total length at birth (Branch 1998); I captured two neonates (both males) measuring 333 and 322 mm TL on the 5th and 26th of July, respectively (months after expected parturition by females). Fresh umbilical scars were present on both individuals. No gravid females were tracked during this study, so ecological information for this subset of the population remains speculative. If gravid *B. gabonica* share biological similarities with other gravid viperids (e.g. extended basking periods and obligate anorexia, Mallow 2003) it is probable that female *B. gabonica* reduce movement and feeding during gestation, but this requires verification.

A recent study by Clark (2006) implemented fixed videography to study the predation behaviour of *Crotalus horridus.* Given that *B. gabonica* spend extended periods of time waiting in ambush for prey and show strong hunting site fidelity, the use of fixed videography would allow the foraging ecology of *B. gabonica* to be analyzed by indirectly recording foraging effort, prey encounter rates, feeding success and hunting times. The "large-prey" hypothesis of Chapter 5 could be empirically tested, and the size and type of prey targeted and consumed could be documented. If such a study were to be done for *B. gabonica* both inside and outside of protected area, availability of preferred prey could be shown, which would allow for better evaluation of *B. gabonica* habitat. Fixed videography would also give valuable insight into other facets of *B. gabonica* ecology, such as

basking behaviour, tolerance to disturbance and interactions with potential predators. In addition to fixed videography, if the doubly labelled water method (Beaupre 1996; Beaupre 2008) was used to measure field metabolic rates and water fluxes, the bioenergetics and foraging ecology of *B. gabonica* could be comprehensively documented.

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The Gaboon Adder (*Bitis gabonica*) in iSimangaliso: a conservation handbook

Jonathan Warner

The Gaboon Adder (isiZulu: *umanqunjwana*) is one of sixty snake species found in the iSimangaliso Wetland Park. Gaboon Adders are renowned for their conspicuous geometric patterning, heavyset appearance and potent venom. Very docile by nature, Gaboon Adders spend most of their time hidden in forest leaf litter. Like many other snakes, Gaboon Adders are successful predators that are an important component of their ecosystem. The species is 'red-listed' in South Africa as 'Vulnerable' and provincially protected in KwaZulu-Natal (Ordinance 15 of 1974). It is also a flagship species of the forest ecoregion in South Africa; the smallest and arguably most vulnerable biome in the country.

In South Africa, Gaboon Adders are restricted to areas north of Mtunzini in subtropical forest habitat. Once suspected to be relatively common in lowland forests such as Dukuduku and Manguzi, the species is now primarily restricted to the Coastal Dune Forest corridor. Most of the South African population is found within iSimangaliso, and Gaboon Adders have been recorded in all sections of the Park except uMkhuze and False Bay (although it probably occurs in the latter).

This document intends to provide information on Gaboon Adder ecology and conservation that will assist park management and staff in protecting the iSimangaliso population through practical means, and to safely interact with the snakes when necessary. Specifically, four main topics are addressed:

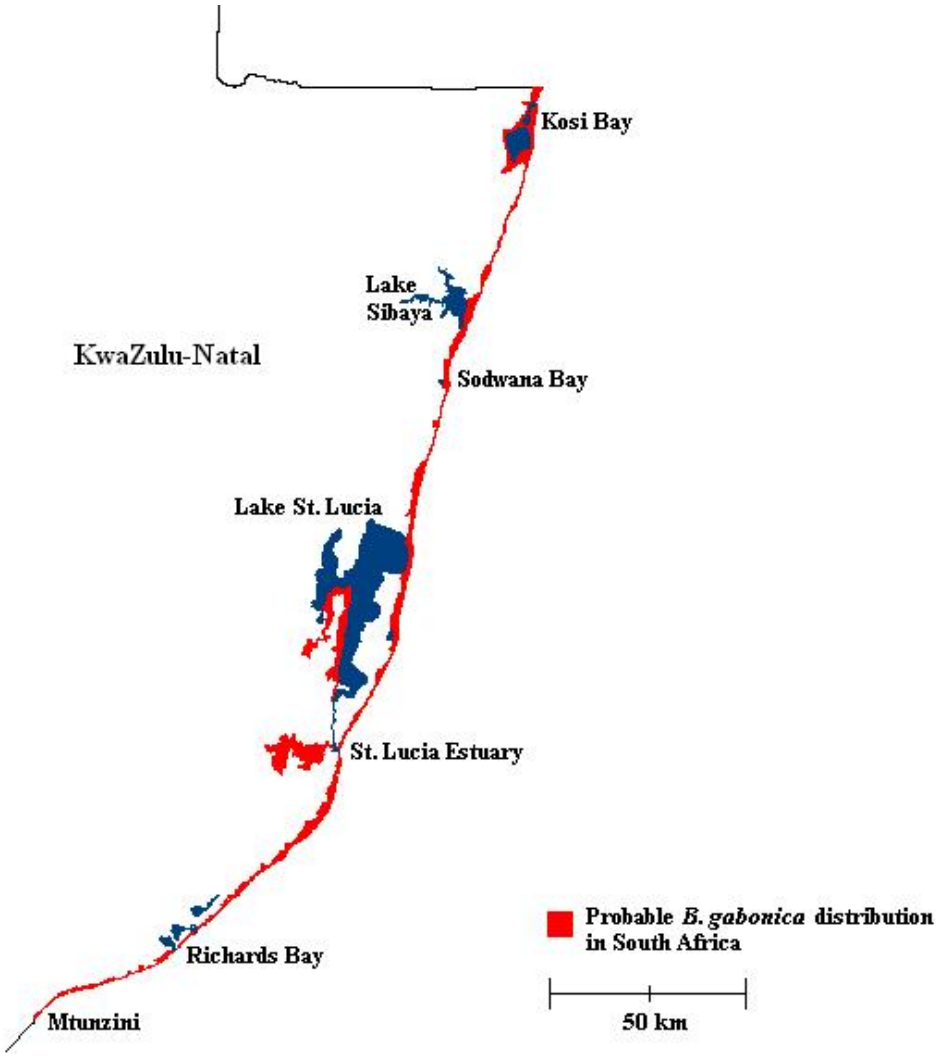
Section A: Ecology

Section B: Threats to Gaboon Adders and Protective Measures for the Species

Section C: Handling and Relocation

Section D: Risk Aversion and Bite Protocol





Inferred distribution of Gaboon Adders in South Africa extrapolated from historical recordings and remaining suitable habitat.

Section A: Ecology

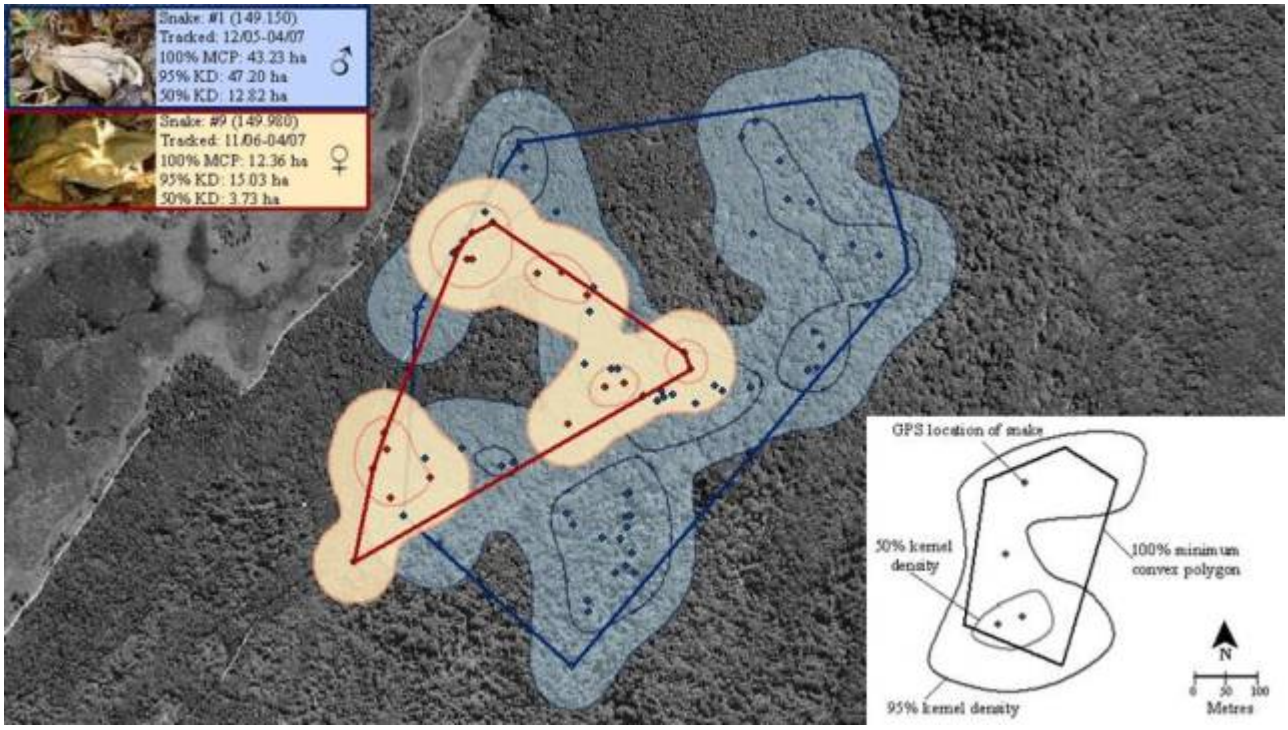
Gaboon Adders are unlikely to be confused with any other snake in iSimangaliso, with the exception of the Puff Adder (*Bitis arietans*); the only other large-bodied adder in the area. Unlike Gaboon Adders, Puff Adders do not occur in forested areas, but the two species occasionally overlap in the transitional zones between subtropical forest and savanna, woodland and grassland. Adult Gaboon Adders in South Africa are larger than adult Puff Adders, and Gaboon Adders can easily be distinguished by their pale-coloured heads and "cigar"-shaped blotches that extend down the length of the spine.



Adult Puff Adder (left) and Gaboon Adder from Dukuduku. Note differences in size, patterning and colour.

Movement Patterns

In general, male Gaboon Adders move more frequently and have larger home ranges than do females. Males can have home ranges exceeding 40 ha, while female home ranges are generally 10 ha or less. Typical movement behaviour of Gaboon Adders consists of occasional small movements (< 15 m) within a particular area (although the time between these minor moves could be several days to several weeks), interspersed by occasional longer, continuous moves (> 50 m). Although distances moved and area of home ranges varies among individuals, a bimodal seasonal activity pattern exists, with movement peaks in the spring and fall. The fall activity peak is associated with the mating season, which occurs March-May in South Africa. During this time, Gaboon Adders are seen (and killed) crossing roads and found in residential gardens, and individuals have been known to move over 500 metres within 24 hrs.



Typical home range estimates for male and female Gaboon Adders.

Gaboon Adders become extremely inactive (but do not hibernate) during the winter months (June-August). During this period, individuals often remain immobile for months at a time at a single location (up to three months). A spring peak in activity follows the winter months and extends into the early summer, but activity generally decreases as the hot summer months continue, resulting in periods of limited or no movement before the fall breeding season commences.

Habitat Use

Gaboon Adders are strongly associated with forest. In iSimangaliso, this habitat includes the lowland, swamp and dune forests found on the coastal plain. Use of forested areas by Gaboon Adders is driven primarily by food acquisition, predator avoidance and thermal requirements. Habitat selection is therefore a trade-off between these three essential factors. During summer months, Gaboon Adders primarily occupy interior regions of the forest, usually selecting areas of dense thicket and thick understory growth (e.g. *Isoglossa* patches). However, during the winter months, they are found in areas of relative open-canopy, including forest patches, forest edge and adjacent woodland and grassland habitats. These areas allow the thermoregulatory needs of Gaboon Adders to be met during cooler weather.



Examples of non-winter habitat: thickets within interior coastal forest areas.



Examples of winter habitat: forest edge and secondary grassland. Note lack of overhead canopy cover.

Diet

Gaboon Adders catch prey by ambush and are probably the most sedentary type of snake in the world. Outside of protected areas where game is scarce, their diet consists primarily of rodents, and occasionally, birds. Within iSimangaliso, Gaboon Adders still opportunistically prey on rodents and other small animals, but they utilize ungulate trails for hunting and will consume prey that may even exceed their own body mass. They have been recorded eating Red Duiker, Genet, and Banded Mongoose, and are likely to prey on any mammals of appropriate size. The unique morphology of Gaboon Adders allow for consumption of these large meals; large heads, stocky bodies, large fangs and high venom yields afford Gaboon Adders dietary options that are unavailable to most other snakes. Gaboon Adders generally feed very infrequently and cease feeding altogether during winter. They shed their skin about twice a year.



Camouflage helps Gaboon Adders blend into leaf litter while waiting to ambush their prey.

Section B: Threats to Gaboon Adders and Protective Measures for the Species

♦ **Habitat Destruction –** In South Africa, most suitable habitat for the species outside of protected area has been destroyed or is in the process of undergoing transformation/fragmentation by humans. Specific activities include informal settlements (e.g., Dukuduku), unnatural burning regimes, agricultural activities and development.

♦ **Alien Invasive Plants –** *Chromolaena odorata* is the primary alien invasive threat to Gaboon Adder habitat. The species is widespread in the Park, but occurs in varying densities. *Chromolaena* chokes out natural vegetation in forest thickets and forest edge, creating unsuitable thermal and feeding conditions for Gaboon Adders. Like many indigenous species, the snakes appear to avoid *Chromolaena* infested areas. *Psidium guajava* (Guava) poses a lesser threat to the species, as it is usually found in open-canopied areas (e.g. secondary grassland on Eastern Shores). Gaboon Adders are occasionally found close to Guava patches during the winter months when individuals require less dense vegetation in order to thermoregulate.

♦ **Illegal Collection –** Gaboon Adders are popular among reptile enthusiasts. This has led to establishment of black market trade for the species in South Africa. Although the market price for wild Gaboon Adders has decreased during the last 15 years, illegal collecting and selling of individuals continues in the Dukuduku area.

♦ **Disease –** Gaboon Adders are prone to cloacal infections and septicemia when kept in captivity, especially when housed with other individuals or stressed. The incidence of such infections among wild individuals appears to be low, but this could change if captive Gaboon Adders escape or are released into the wild. Additionally, legally imported Gaboon Adders from other African countries could pose disease- and genetic-related threats if ever introduced to the wild South African population.

♦ **Road Mortality –** This is a threat to many reptiles, both inside and outside of the Park. Gaboon Adders are most likely to be encountered on roads during dusk or at night, especially during the fall breeding season (March-May). Because Gaboon Adders are slow-moving, they are at high risk when crossing roads.

♦ **Indiscriminate Killing –** Gaboon Adders encountered by people from the local community are often killed. Killing is almost always opportunistic and occurs when snakes are discovered in close proximity to residences. Gaboon Adders have been reported to feed on domestic chickens, providing additional economic motive for indiscriminate killing.

♦ **Umuthi** – In Zululand, the skin and organs of Gaboon Adders are sold and used for ‘muthi (traditional medicine). The occurrence of this is probably variable in communities adjacent to the Park, and the number of snakes harvested for ‘muthi is unknown.

Ecological evidence and distributional data suggest the iSimangaliso Gaboon Adder population currently exists at a density that is 'normal' for the area, and appears to be healthy. The greatest threat to the survival of the species in South Africa is destruction and fragmentation of coastal forest. iSimangaliso is the largest protected refuge for Gaboon Adders in southern Africa. **Maintaining the continuity and integrity of the entire iSimangaliso dune forest corridor is the most critical protective measure needed for Gaboon Adder conservation.** Currently this condition is being met throughout the Park; for the most part, benign management of the species appears to be effective. Nonetheless, continued intentional habitat protection is necessary for the long-term viability of the species in South Africa.

Current EKZNW policy of "spot-burning" (as opposed to block burning) does not appear to constitute a significant threat to Gaboon Adders in iSimangaliso. However, because Gaboon Adders (and many other forest-adapted species) utilize the forest ecotone – particularly during winter – it is important that the forest edge is burned sporadically and not in successive years, allowing for natural succession of the ecotone plant community after a fire. Additionally, extensive areas of forest edge and immediately adjacent habitats (e.g., woodland, grassland) should not be burned simultaneously, since this is likely to cause high mortality in localized areas. Burning to reduce forest encroachment in some areas of the park (e.g., Eastern Shores) does not presumably present serious risk to the species, as long as such burns are rotated and not systemically applied to the entire ecotone.

Due to the conservation and collector value of Gaboon Adders, the need for a captive breeding facility has been a frequently raised topic by members of the public in recent years. Such a facility would presumably provide a.) Gaboon Adders for purchase by licensed buyers, and b.) Gaboon Adders available for repatriation purposes in suitable habitat.

In 2006, a Gaboon Adder breeding/holding facility at 121 Battalion was shut down by EKZNW after permit conditions were not met. Subsequent to the closure of the 121 facility, six of the eight Gaboon Adders confiscated required urgent medical treatment due to advanced septicaemia and/or malnourishment. Since 2006, no further Gaboon Adder permits have been granted to any member of the public.

At this moment in time, a captive breeding facility is not recommended on the grounds that:

1.) Currently, the South African and global market for pet Gaboon Adders by all measures appears to be stable, and "legal" Gaboon Adders can be obtained without difficulty from private breeders.

2.) South African Gaboon Adders have consistently been shown to do poorly in captivity when stressed or housed with multiple individuals.

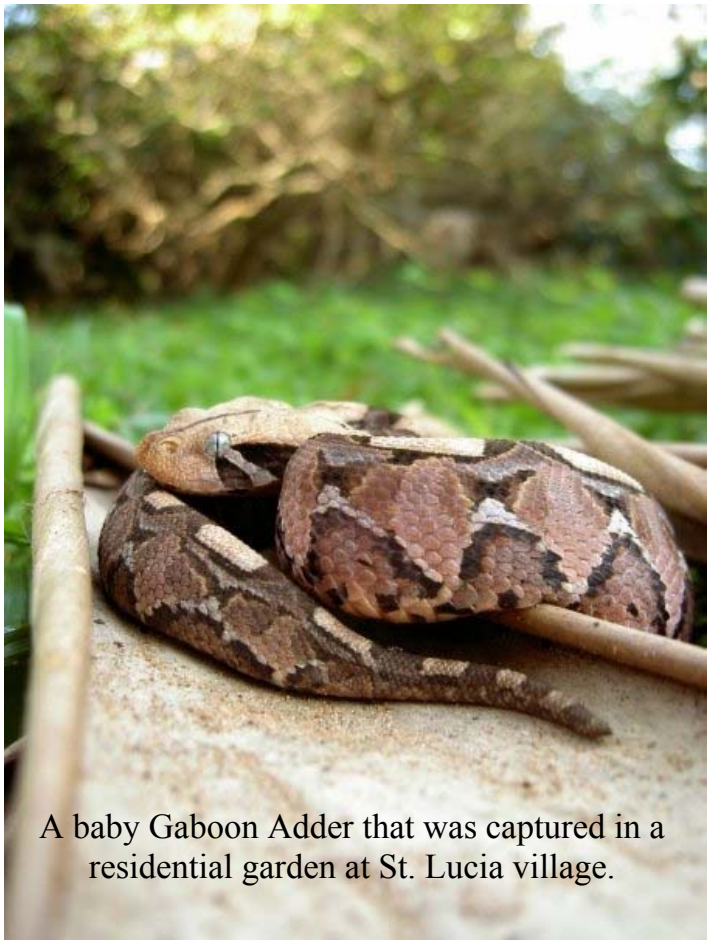
3.) Recent attempts to create a sustainable breeding facility for the species have failed.

4.) There is no evidence that any area within the species' distribution requires repatriation, and "restocking" efforts could pose genetic and epidemiological threats to the natural Gaboon Adder population.

Currently, the main benefit of a facility that holds captive Gaboon Adders is educational, as the species is a charismatic part of the indigenous reptile fauna and a source of public interest. Currently, the Crocodile Centre in St. Lucia has one individual available for public viewing, and has facilities for one or two more individuals.

Section C: Handling and Relocation

Occasionally, a situation arises that necessitates Park staff having to capture a Gaboon Adder because it is discovered in close in proximity to people. Gaboon Adders are most frequently encountered by people during the breeding season (roughly March-May) when snakes move over extended during mate searching. During this time they are occasionally seen in unprotected areas (primarily St. Lucia Village, Dukuduku and Mtunzini), usually in local gardens or on roads. Due to public concern, Park liability and the conservation value of the species, Gaboon Adders found outside the Park have been deemed by EKZNW as candidates for relocation.



A baby Gaboon Adder that was captured in a residential garden at St. Lucia village.

The handling of Gaboon Adders should be done under controlled circumstances, only by capable personnel. Gaboon Adders are sluggish snakes, but are capable of fast strikes and therefore must be handled with great care:

1.) Slowly approach the Gaboon Adder from the side or rear. Do not get closer than one body length of the snake.

2.) Use a suitable-sized implement (e.g., hook, spade, knobkerrie) to scoop the snake off the ground at the midsection of the body.

3.) Carefully transport the Gaboon Adder to an appropriate container (e.g., bucket, plastic tub).

4.) Do not curl fingers underneath the lid while securing it to the container.

After capture, Gaboon Adders should be relocated and released as soon as possible. The following management decisions have been made by EKZNW in regards to relocating Gaboon Adders:

Situation	Action
Gaboon Adder encountered inside Park	Leave individual undisturbed and record locality of encounter.
Gaboon Adder encountered inside Park, but in close proximity to humans (campsite, staff quarters, etc.)	Relocate individual within the Park. Release in indigenous forest nearest to capture area.
Gaboon Adder encountered outside Park in Umtunzini area	Relocate individual to Western Shores. Release in indigenous forest in northern (protected) section of the Dukuduku Forest, at least 2 km from R618 tar road.
Gaboon Adder encountered outside Park in Dukuduku area	Relocate individual to Western Shores. Release in indigenous forest in northern (protected) section of the Dukuduku Forest, at least 2 km from R618 tar road.
Gaboon Adder encountered outside Park in St. Lucia area	Relocate individual to Eastern Shores. Release in dune forest at least 2km from St. Lucia village.
Gaboon Adder encountered outside Park in area other than Umtunzini, Dukuduku or St. Lucia	Relocate individual to the Park. Release in indigenous forest, at least 2 km from nearest Park border.

Section D: Risk Mitigation and Bite Protocol

Gaboon Adder bites, although potentially deadly, are extremely rare. Most recorded bites are from mishandling by snake collectors and zookeepers. Because Gaboon Adders are extremely docile animals and do not occur in high densities, the risk the species poses to Park staff, and the general public, is extremely low. Of the nine potentially deadly species that occur in the Park, Gaboon Adders are of the least concern in regards to human threat. Most snakebites in Zululand are from Puff Adders, Night Adders and Mozambique Spitting Cobras (‘Mfezi). The biggest risk posed to humans by Gaboon Adders is a bite after a snake has been stepped on; a scenario of undocumented occurrence in iSimangaliso by a member of the public. Nevertheless, certain precautions should be taken by people when working in forested areas in the Park:

♦ When working or walking in the field, wear closed-toe shoes (preferably leather boots that cover the ankle). A Gaboon Adder bite is most likely to be inflicted on the lower leg.

♦ When inside forested areas, avoid unnecessary activity inside dense thickets and areas of thick understory growth.

♦ Workers clearing bush should always look carefully before cutting and picking up vegetation in thickets or on the forest floor.

♦ Gaboon Adders (and Puff Adders) hiss loudly when threatened. Slowly back away if this noise is detected. Snakes do not chase people.

♦ If a Gaboon Adder is encountered in the field, keep at least 2 m away from the snake and do not physically disturb it.

♦ If encountered on a road, do not ‘straddle’ a Gaboon Adder with the vehicle in order to get past. Wait until the snake successfully moves across.

♦ Never try to pick up a Gaboon Adder with your bare hands, even if it appears calm.

♦ Never taunt or try to kill a Gaboon Adder.

In the event of a Gaboon Adder bite, it is critical that the victim remains calm and gets to a medical facility as quickly as possible. Gaboon Adders have long fangs that are capable of injecting large quantities of cytotoxic venom, which can cause intense pain, swelling, blistering, and ultimately organ failure and death. However, symptoms are variable and depend on the severity of the bite (snakes have control over how much venom they inject) and the health of the person bitten. In all but the most severe cases, the victim has *at least* 2-3 hours to get medical treatment before a bite becomes life-threatening. Considering the distribution of the species in KwaZulu-Natal, this means that most Gaboon Adder bites allow time for the victim to be transported (by air or land) to Richards Bay Hospital (Tel: 035 780 6111) before the onset of serious symptoms.

A bite from a Gaboon Adder should always be considered a medical emergency, and getting treatment quickly can not only prevent death, but also minimize the effects of the bite and shorten the recovery process. In the time period before the victim is able to get medical assistance, there are certain things they should refrain from doing:

♦ **Do not** undergo any unnecessary movements. Keep walking to a minimum. Activity speeds the transport of the venom to the body.

♦ **Do not** try to catch or kill the snake. This will only increase the chance of another bite.

♦ **Do not** apply a tourniquet or pressure bandage to the bite. Because Gaboon Adder venom is cytotoxic, this will increase local tissue damage and may result in limb/digit amputation.

♦ **Do not** cut, bleed, suck or apply electrical shock therapy to the bite. These techniques have been proven ineffective as first-aid measures and can even worsen the injury.

♦ **Do not** drink alcohol after being bitten, as this widens blood vessels and can quicken serious symptoms.

♦ **Do not** substitute immediate treatment in a hospital for traditional medical remedies.

♦ **Do not** administer antivenom before reaching the hospital. Gaboon Adder bites usually require a much higher dosage than what is commercially available in first-aid kits, and an allergic reaction to antivenom can kill the victim more quickly than the venom can.