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Source: Copeia, 2012(1):115-120. 2012.
Published By: The American Society of Ichthyologists and Herpetologists
DOI: http://dx.doi.org/10.1643/CH-11-048
URL: http://www.bioone.org/doi/full/10.1643/CH-11-048

Copeia 2012, No. 1, 115–120

Dwarfs on the Move: Spatial Ecology of the World's Smallest Viper, *Bitis schneideri*

Bryan Maritz[1] and Graham J. Alexander[1]

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

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

Namaqua Dwarf Adders (*Bitis schneideri*) are arid-adapted viperids that inhabit semi-vegetated coastal sand dunes along the southern African western coast (Broadley, 1983; Branch, 1998). Individuals of this species are recognized as the smallest viperids, reaching a maximum snout–vent length of no more than 255 mm (Branch, 1998; Maritz and Alexander, 2011). Our unpublished data also demonstrate that individuals occur at high population densities. *Bitis schneideri* is currently listed as Vulnerable by the IUCN (Branch, 1988; World Conservation Monitoring Centre, 1996). However, recent assessments, based on the discovery of additional localities and our ongoing ecological investigations indicate that the IUCN conservation status may change to that of Least Concern in the future. Nonetheless, information regarding the ecology of this species is of value to conservation managers because the fauna of the region (especially typical species such as *B. schneideri*, which is endemic to part of the Succulent Karoo) remains poorly known. Additionally, ecological information from a wide range of species is needed to develop the holistic understanding of arid ecosystem processes required to conserve and manage such environments.

Movement patterns are an important component of the ecology of all animals (Nathan, 2008). In snakes, movement allows individuals to find feeding grounds (King and Duvall, 1990; Webb and Shine, 1997), thermally suitable retreats (Webb and Shine, 1998), overwintering sites (King and Duvall, 1990; Secor, 1994), and mates (Madsen et al., 1993). Moreover, measures of space-use can provide valuable insights into mating systems (Shine et al., 2001), risk of mortality (Bonnet et al., 1999), and conservation issues such as gene flow and habitat fragmentation (Clark et al., 2008). As a result, studies focusing on space-use by snakes, and snake ecology in general, have become increasingly popular in recent years (Shine and Bonnet, 2000). However, studies of the spatial ecology of snakes suffer from a strong geographic (and thus phylogenetic) bias as the vast majority are concerned with species inhabiting the Americas, Europe, and Australia. Despite Africa's rich snake fauna (Greene, 1997), the spatial ecology of relatively few African snake species has been investigated. While there is an abundance of radio-telemetric studies on snakes in general, fewer than ten have focussed on African snake species (Angelici et al., 2000a, 2000b; Lawson, 2006; Linn et al., 2006; Alexander, 2007; Cottone, 2007; Warner, 2009).

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

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Submitted: 8 April 2011. Accepted: 7 November 2011. Associate Editor: D. Kizirian.

DOI: 10.1643/CH-11-048

Table 1. Number of Individuals, Snout–Vent Length (SVL), Mass, and Duration of Observation for 37 *Bitis schneideri* Fitted with Radio Transmitters.

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

smallest viper can provide valuable insight into the evolution of this and other ‘dwarf’ species.

MATERIALS AND METHODS

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

Radio-telemetry.—We used radio-telemetry to investigate movement patterns of 18 female and 19 male adult individuals (Table 1). We actively searched for and captured snakes on the study site, anesthetized them using vaporized isoflurane, and fitted each with a temperature sensitive radio-frequency transmitter (BD-2NT, Holohil Systems Limited, mass = 0.5 g). Transmitters were glued to the dorsal surface of the snakes using a cyanoacrylate adhesive, and were positioned slightly anterior to the tail, with the 140 mm whip antenna trailing behind the snake (Fig. 1). Although we did not quantify differences between telemetered and non-telemetered snakes, transmitters did not appear to influence movement, behavior, or retreat site selection. Only adult individuals were fitted with transmitters to ensure that transmitter mass remained below 5% of snake body mass. As a consequence of their small size, transmitters had short life-spans (21 days at 40°C; according to manufacturer specifications). For this reason, and in order to quantify differences in seasonal movement patterns, telemetry work was performed on three groups of snakes during three austral seasons: spring (October 2009), summer (December 2008–January 2009), and winter (July 2010; Table 1).

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

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

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

Juvenile movement.—As juveniles of this species are too small to carry transmitters (mean juvenile mass = 4.1 ± 0.9 g; Maritz and Alexander, 2011), we compared MDD of adult and juvenile snakes recaptured during a mark–recapture study. Search methods involved active searches for snakes across a 22 ha and a 16 ha plot on our study site. Survey effort totalled 629 observer hours over three consecutive austral summers (generally daily from September to March) beginning in September 2007. Each individual captured in the mark–recapture program was sexed by assessing relative tail length (Maritz and Alexander, 2011), marked by clipping ventral scales (Fitch, 1987), weighed, measured, and released at the point of capture which was recorded on a handheld GPS device (Garmin Etrex; datum: WGS84). For each recaptured individual, we recorded the straight-line displacement from the original point of capture using a GPS and the time interval between captures (number of days). Given the size of the study plots, our methods allowed us to detect displacements of between 0 m and approximately 900 m and 660 m for each plot, respectively (equal to the longest axis of each plot). We calculated MDD as the total displacement (m) between captures over the duration between captures (days), and compared these measures between adult males, adult females, and juveniles using analysis of variance.

RESULTS

Radio-telemetry.—Mean daily displacement of telemetered snakes varied significantly across sexes and seasons (Factorial

Fig. 1. Coastal Sandveld habitat at our study site (A), and adult male *Bitis schneideri* fitted with an externally attached radio-transmitter (B), and an adult male *B. schneideri* fitted with a radio-transmitter in the process of ingesting a Namaqua Rain Frog (*Breviceps namaquensis*).

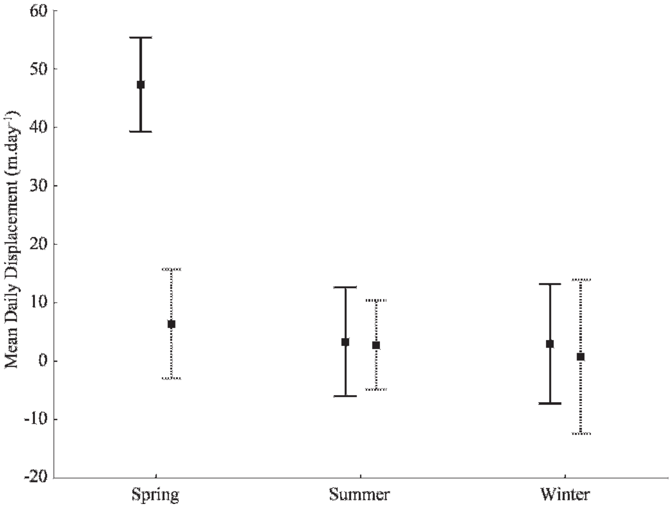

Fig. 2. Mean daily displacement (MDD; m.day^{-1}) of female (dashed) and male (solid) telemetered *Bitis schneideri* during austral spring, summer, and winter. Error bars represent 95% confidence intervals.

ANOVA: $F_{2,31} = 6.27$, $P < 0.01$, Fig. 2). Tukey HSD *post-hoc* analysis revealed that during spring the MDD of male snakes (47.3 ± 3.9 m.day^{-1}) was significantly higher than the MDD of females during spring (6.4 ± 4.6 m.day^{-1}), summer (2.7 ± 3.7 m.day^{-1}), and winter (0.8 ± 6.5 m.day^{-1}), and males during summer (3.3 ± 4.6 m.day^{-1}) and winter (3.0 ± 5.0 m.day^{-1}), which were all similar.

Home range estimation.—Mean squared displacement from the center of activity range varied significantly among individuals (ANOVA: $F_{36,663} = 31.03$, $P < 0.001$), but estimated home range was not significantly related to the number of observations of each individual (Spearman's Rank Order Correlation: R = 0.064). Estimates of home range area exhibited large variation and were not significantly different from one another (Factorial ANOVA: $F_{2,31} = 3.18$, $P = 0.055$, Fig. 3), although Tukey *post-hoc* analysis revealed that MSD of males during spring was significantly higher than all other measures of MSD. Males exhibited the largest home ranges (1.07 ± 0.21 ha) during spring. Home range estimates for males in summer (0.02 ± 0.25 ha) and winter (0.02 ± 0.27 ha) were similar to those of females during spring (0.02 ± 0.25 ha), summer (0.02 ± 0.20 ha), and winter (0.001 ± 0.35 ha). Area estimates of home ranges of females snakes (mean ± SE = 0.10 ± 0.09 ha; max = 0.28 ha) were significantly smaller (ANOVA: $F_{1,698} = 39.67$, $P < 0.001$) than the home ranges of male snakes (mean ± SE = 0.85 ± 0.09 ha; max = 1.03 ha).

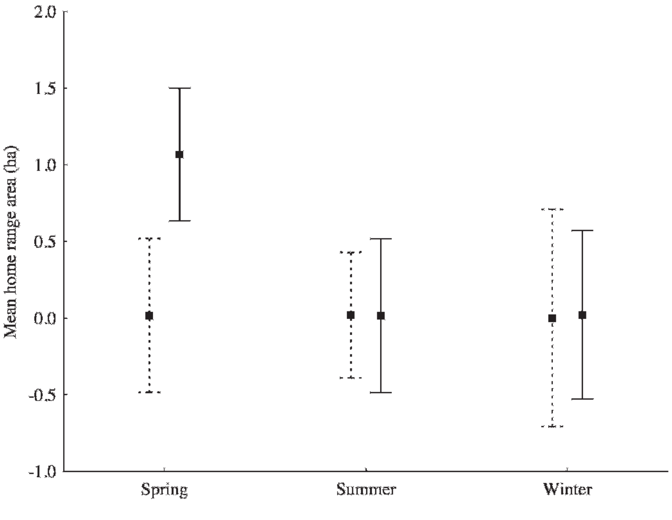

Fig. 3. Mean home range area estimates for male (solid) and female (dashed) telemetered *Bitis schneideri* during austral spring, summer, and winter. Error bars represent 95% confidence intervals.

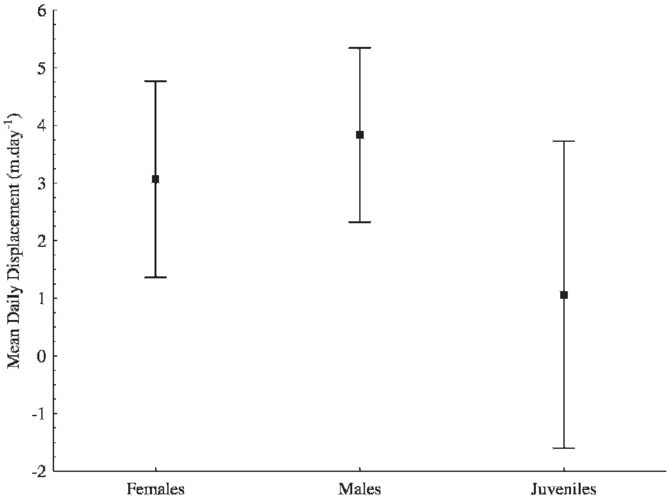

Fig. 4. Mean daily displacement (m.day^{-1}) of recaptured adult female, adult male, and juvenile *Bitis schneideri*. Error bars represent 95% confidence intervals.

Juvenile movement.—Active searches on our study site produced 340 individual *B. schneideri* (134 females, 145 males, 61 juveniles) of which 60 (23 females, 28 males, 9 juveniles) were recaptured at least once. ANOVA did not detect any significant differences in the MDD of adult females, adult males, and juveniles (ANOVA: $F_{2,56} = 2.58$, $P = 0.08$, Fig. 4). MDD for males (3.8 ± 0.7 m.day^{-1}) and females (3.1 ± 0.8 m.day^{-1}) were similar and generally greater than the MDD for juveniles (1.1 ± 1.3 m.day^{-1}).

DISCUSSION

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

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

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

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

In general, the individuals of smaller-bodied species tend to occupy smaller home ranges than do individuals of larger-bodied species (Mace et al., 1984; but see MaCartney, 1988). Thus, the small home ranges that we measured for *B. schneideri* are not surprising. However, the small size of *B. schneideri* means that directly comparative home range area estimates are not readily available. Work on *Crotalus cerastes* (Secor, 1994) and *Sistrurus catenatus* (Marshall et al., 2006) showed that some small pitvipers have comparatively large home ranges. Several other species of pitvipers are known to use small home ranges: the asian *Gloydius shedaoensis* has home ranges of <0.3 ha (Shine et al., 2003), and the small and arid adapted *Crotalus pricei* has a home range of 0.2–2.3 ha (Prival et al., 2002). The elapid, *Hoplocephalus bungaroides* also exhibited relatively small home ranges, with adults occupying mean home range areas of 3.3 ha (Webb and Shine, 1997).

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

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

ACKNOWLEDGMENTS

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

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