Movement Patterns in the Smallest Viper, *Bitis schneideri*

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Moving from one location to another provides animals with obvious benefits, but also incurs costs. When and how far an animal chooses to move is thus of fundamental importance to all aspects of its biology. We investigated movement patterns in a population of Namaqua Dwarf Adders (*Bitis schneideri*) in southern Africa through the use of radio telemetry. We measured how many individuals moved at different times of the day, at different times of the year, and differences in displacement frequency between sexes. We also assessed the influence of environmental variables (air temperature, relative humidity, atmospheric pressure, and wind speed) on activity levels. Snakes moved almost exclusively during the day-light hours, despite our expectations from the literature. Namaqua Dwarf Adders show limited seasonal variation in activity levels, with males moving more frequently during spring months than in other seasons. Our analysis indicated that movement was linked most closely to environmental conditions during the winter season, when conditions were generally less suitable for movement. We hypothesize that the observed variation in movement patterns at all temporal scales is the result of the selective pressure imposed by the costs of activity during sub-optimal environmental conditions.

MOVEMENT, defined here as the displacement of an animal from one location to another, has important implications for organisms and is necessary for all aspects of their biology (Nathan, 2008). Moreover, the decision to move represents the trade-off between the advantages of moving at a particular time, and the cost associated with that movement (Metcalfe et al., 1999). Thus, it is not surprising that many organisms vary the timing of movements to maximize the associated benefits and minimize the costs. The selective pressure provided by such costs and benefits means that movement is often at least partly synchronized within a population, resulting in predicable patterns (Alexander and Marshall, 1998). Investigating activity patterns of organisms can help elucidate the ecological pressures experienced by organisms (Bonnet et al., 1999) and the evolutionary history of those species (Luiselli, 2001). Studies of activity patterns can also provide estimates of the variation in detection probability of individuals within a population (Sun et al., 2001).

Information regarding activity patterns of organisms is essential for understanding their life-history and ecology, and thus developing adequate conservation and management plans (Dodd et al., 2004). It is therefore unsurprising that studies of activity patterns are common (Gibbons and Bennet, 1974; Aichinger, 1987; Doran, 1997; Speakman et al., 2000). Even within taxonomic groups that are difficult to study, such as snakes (Shine and Bonnet, 2000), studies describing activity patterns and the environmental correlates of activity patterns have proliferated (Shine, 1979; Gibbons and Semlitch, 1987; Daltry et al., 1998). Few studies, however, have investigated activity patterns in African snakes (e.g., Alexander, 1997; Alexander and Marshall, 1998) leaving an obvious gap in our knowledge.

We aimed to improve our understanding of the ecology of the small-bodied African viperid *Bitis schneideri* by investigating variations in their activity patterns through the use of radio telemetry. Because *B. schneideri* is an ambush predator, quantifying the degree to which resting time and foraging time is partitioned is impossible (resting positions and ambush positions are usually indistinguishable). We therefore investigated frequency of movement, rather than activity patterns in general. Specifically we aimed to investigate 1) when, during the diel cycle, individuals were most likely to move, 2) whether there was seasonal or sexual variation in the frequency of movement, and 3) the degree to which the observed patterns of activity were related to environmental conditions. In accordance with the ecology of most temperate snakes, we predicted that patterns of movement would show seasonal variation associated with environmental suitability, as well as sex-based differences associated with mating behaviors.

MATERIALS AND METHODS

Study animal.—*Bitis schneideri* is the smallest viper (mean SVL = 200 mm; max SVL = 254 mm). It is arid-adapted and inhabits coastal dune systems along the southern Africa west coast (Broadley, 1983; Branch, 1998). Until recently the species was very poorly known and was listed as Vulnerable by the IUCN (Branch, 1988; World Conservation Monitoring Centre, 1996) as a result of extensive strip mining within its restricted distribution. However, our recent work has shown that it is relatively abundant in parts of its range (Maritz, 2011; Maritz and Alexander, 2012a), resulting in it being re-evaluated as Least Concern (Bates et al., in press). Like most viperids, *B. schneideri* is an ambush predator and individuals thus tend to be relatively sedentary compared to actively foraging snakes. Although little is known about which factors influence the likelihood of movement in *B. schneideri*, risk of avian predation may be important (Maritz and Scott, 2010).

Study site.—Our study site falls within the Succulent Karoo Biome (Mucina and Rutherford, 2006) of southern Africa, one of two globally recognized, arid biodiversity hotspots (Myers et al., 2000). All investigations took place on the farm Noup (30°08′S, 17°12′E), Northern Cape Province, South Africa. The study site receives less than 150 mm rainfall per annum, but coastal fog is frequent (Cowling et al., 1999). More than 60% of the annual rainfall falls during winter (Desmet, 2007). The climate at the study site is temperate with relatively small differences in temperatures between the seasons due to the close proximity and moderating effect of the cold Benguela Current. The habitat and environmental conditions on the study site are

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Table 1. Number of Individuals ($n_{individuals}$), Mean ± SD Duration of Telemetry (Days), and Total Number of Observations ($n_{observations}$) of Radio-telemetered *Bitis schneideri* in Each Season of Our Study.

	Spring		Summer		Winter	
	Male	Female	Male	Female	Male	Female
$n_{individuals}$	8	6	6	9	5	3
Duration (days)	15.0 ± 2.3	10.3 ± 6.1	17.2 ± 5.5	22.0 ± 2.6	18.2 ± 1.1	17.7 ± 1.5
$n_{observations}$	120	62	103	198	91	53

representative of those across the distribution of *B. schneideri*. Temperatures are cool, ranging from a mean daily temperature of 14.3°C in winter to 18.2°C in summer (Desmet, 2007). The habitat in the area is relatively homogeneous and consists primarily of semi-vegetated, longitudinal aeolian dunes, dominated by sclerophyllous shrubs and succulents (Mucina and Rutherford, 2006).

Radio telemetry.—We actively searched for and captured 37 adult *B. schneideri* from the study site for radio-telemetry work (Table 1). Transmitters (BD-2NT, Holohil Systems Limited) were attached using a cyanoacrylate adhesive to the dorsal surface of the snakes slightly anterior to the tail, so that the 140 mm whip antenna trailed behind the snake. We used small, lightweight transmitters (0.55 g) because of the small body size of *B. schneideri* and thus were limited by short battery lives (21 days at 40°C; according to manufacturer specifications) to relatively brief bouts of data collection. Telemetry work was conducted in three sessions; spring (October 2009), summer (December 2008–January 2009), and winter (July 2010; see Maritz and Alexander, 2012b). Each telemetered snake was released at point of capture within seven days of capture (the majority within two days). Snakes were recaptured after 20 days, and after transmitters were removed (in cases where transmitters could not be dislodged, we held snakes until they shed), they were released at final capture site.

Snakes were located daily using a Communications Specialist R1000 hand-held receiver and 3-element Yagi antenna. During each encounter we recorded the time of day and the behavior (moving, resting/ambush) of the snake. We also recorded the location of each snake using a handheld GPS (Garmin eTrex; Datum WGS 1984), and, because the GPS had an error of up to 5 m, we marked each location with orange flagging tape for added precision. We categorized any movement of more than 2 m as a displacement. Finally we measured shaded air temperature at ground level (°C), wind speed approximately 1 m above the ground ($m.s^{-1}$), relative humidity (%), and atmospheric pressure (hPa) using a Kestrel 4000 hand-held weather meter.

Diel movement patterns.—For logistic and practical reasons, telemetry was limited to day-time hours. However, night-time fieldwork totalling more than 50 hours (between 1900–2300 h; primarily during spring and summer months) generally did not reveal active snakes, and only once (during three years of extensive fieldwork) did we locate an active individual at night (a male during spring). In order to empirically assess the likelihood of Namaqua Dwarf Adders moving during the night, we regressed the mean displacement distance of telemetered snakes against the number of day-light hours between observations. Since we located snakes once a day, time between observations also always included one scotoperiod. We calculated hours of daylight using appropriate times for sunset and sunrise, grouped and then averaged displacement measures into 1-hour bins. Our expectation was that if *B. schneideri* is diurnal as our observations suggest, then the displacement of snakes would be positively correlated with the number of daylight hours between observations and the regression line should intercept through zero (i.e., If our hypothesis is correct, zero day-light should result in zero displacement, irrespective of the number of night-time hours). Although this approach assumes a linear relationship between displacement and number of daylight hours, the predicted result is still likely to demonstrate whether snakes are moving during night-time hours. We also assessed variation of activity within the diel cycle by calculating the proportion of snakes that were active when observed during each hour bin in each season. We standardized our measures across seasons so that activity in each hour bin represented a proportion of all activity during that season. Doing so allowed us to compare the overall pattern in diel activity between each season using a Friedman analysis of variance, a non-parametric rank analysis for dependent data.

Sexual and seasonal variation.—We calculated the proportion of days during which snakes moved (total number of days with displacement divided by the total number of days of observation) during each telemetry session and compared this measure (after arcsine transformation) between sexes and seasons using factorial analysis of variance.

Environmental correlates.—We investigated the degree to which environmental variables influenced movement patterns separately for each season using Principal Components Analysis (PCA) to distill the four measured and auto-correlated environmental variables down to two principal components (PC1 and PC2). We then used Student's T-test to compare mean principal component vectors for individuals that were active or not active when observed.

RESULTS

Diel movement patterns.—Namaqua Dwarf Adders moved only during daylight hours. The mean displacement regressed against the number of day-light hours between observations showed a significant relationship (Fig. 1; Regression: y = 0.92x + 1.60; R^2 = 0.47, P = 0.005), and the intercept was close to, and not significantly different, from zero (Intercept of regression: t_{15} = 0.65, P = 0.53; Fig. 1). This indicates that displacement between observations separated by only night-time hours was unlikely, indicative of diurnal activity.

The pattern of diel activity did not differ significantly among the three seasons (Friedman ANOVA: $\chi^2_{9,2}$ = 0.00,

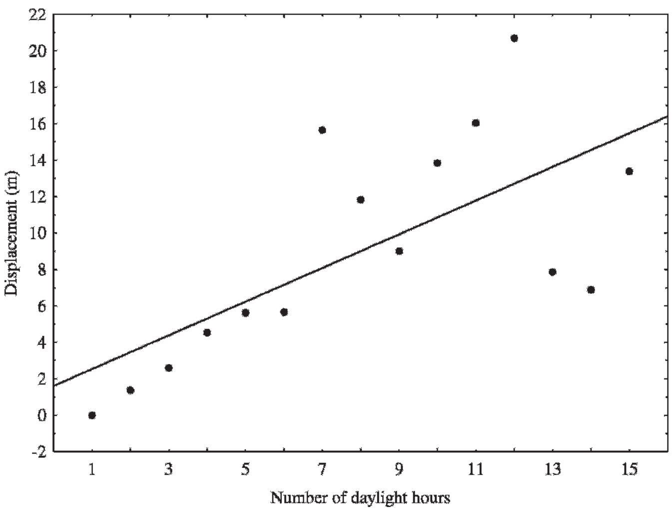

Fig. 1. Linear regression ($y = 0.92x + 1.60$, $R^2 = 0.47$, $P = 0.005$) of the number of daylight hours against the mean displacement of telemetered Namaqua Dwarf Adders between consecutive observations. As predicted, mean displacement of snakes experiencing zero daylight hours was not significantly different from zero.

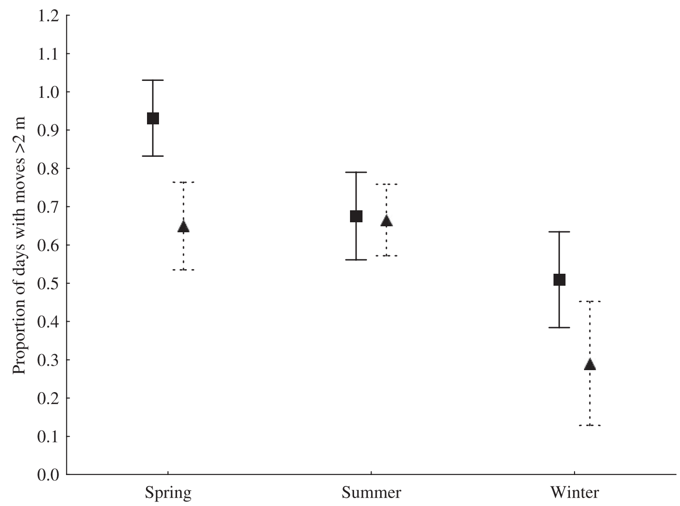

Fig. 3. Proportion of days with movement greater than 2 m for male (solid) and female (dashed) *B. schneideri* during spring, summer, and winter months. Graphs show means and 95% confidence limits.

$P \approx 1.00$). We therefore pooled the data for all three seasons. Activity was not equal across the day, and although limited by variable sampling intensity at different times of the day showed a bimodal peak during midmorning and late afternoon ($\chi^2 = 895.33$, $P < 0.001$; Fig. 2), with snakes apparently avoiding movement during the hottest part of the day. Overall, activity was low; only 10.7% of observations were of active snakes.

Sexual or seasonal variation.—The proportion of days during which male and female snakes moved varied significantly across seasons and between the sexes (ANOVA: $F_{2,31} = 5.26$, $P = 0.01$; Fig. 3). Tukey HSD *post-hoc* analysis revealed that during spring, males (93.1% ± 4.8 of days) moved significantly more often than females (64.9% ± 5.6). However, there were no significant differences between males and females in summer (males 67.1% ± 5.6; females 66.5% ± 4.5) or winter (males 50.9% ± 6.1; females 29.0% ± 7.9). There were also no significant differences among seasons for females, or for males between summer and winter.

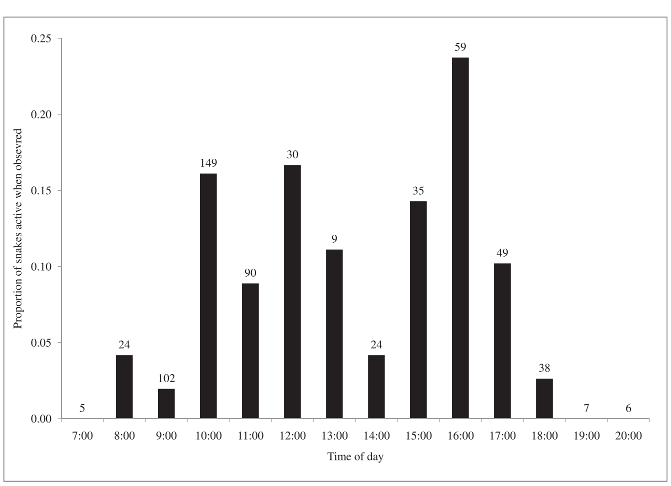

Fig. 2. Proportion of telemetered snakes that were moving when observed during the course of the day. Numbers above bars represent the number of observations.

Environmental correlates.—For each season, the four measured environmental variables were distilled down to two principal components. In all cases, PC1 was dominated by the effects of air temperature and relative humidity, while PC2 was composed primarily of wind speed and atmospheric pressure (Table 2). The degree to which activity correlated with environmental variables differed across seasons. During winter, mean principal component vector for PC1 and PC2 were significantly different between observations of moving and non-moving snakes. During spring, mean principal component vector for PC1 was significantly different between observations of moving and non-moving snakes but not significantly different for PC2. During summer, the mean principal component vectors for observations of moving and non-moving snakes were not significantly different, although differences in PC1 were nearly significant.

DISCUSSION

Our study showed that Namaqua Dwarf Adders are diurnal, sedentary ambush foragers. They moved predominantly during mid-morning and late afternoon, a pattern that prevailed in each season. Generally, sexes had similar movement patterns, but males became more active and moved further than females during spring, probably due to males searching for mates at this time (Maritz and Alexander, 2012a). During winter, when environmental conditions are likely to be suboptimal, activity was limited to periods of suitable temperature and humidity, and to a lesser extent, wind and barometric pressure. Environmental conditions did not appear to be as restrictive in spring and summer, but movement was limited by cold night-time and hot midday temperatures.

Namaqua Dwarf Adders' behavior of cryptically burying just beneath the sand surface while in ambush or at rest meant that we were unable to track snakes during the night without a high probability of disturbing them. Thus, we were limited to measuring activity during hours of daylight,

Table 2. The Factor Coordinates of Each Environmental Variable to Principal Components One and Two, for Each Radio-Telemetry Season, as Well as *F* Test Statistic for the Comparison of Each Principal Component between Active and Non-active Snakes. Values in bold-face are statistically significant ($\alpha = 0.05$).

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

and could not, therefore, directly measure activity levels for night-time hours. However, we overcame this handicap by extrapolating the relationship between displacement and daylight hours. The regression indicates that there was no displacement if daylight is extrapolated to zero. Since snakes were tracked once daily, consecutive measures were always separated by a night. We believe that our approach for measuring night-time activity is novel and could have wider application in other studies. For example, if the study animal is active during the day and night, this method will provide an estimate of how movement is apportioned between the two periods (indicated by the intercept). It also highlights the increased utility of tracking snakes consistently on a daily basis, although the methodology could be applied in studies that track snakes less often, provided that time is recorded with observations.

Our finding that *B. schneideri* moved only during the day was unexpected. Elliptic pupils in snakes, as seen in *B. schneideri*, are usually indicative of a nocturnal lifestyle (Brischoux et al., 2010). Also, Branch (1998) considers *Bitis schneideri* to be nocturnal, although this assessment appears to be based primarily on extrapolation from a better-know closely related species. *Bitis caudalis*, the sister species of *B. schneideri*, is primarily nocturnal (Shine et al., 1998; DeNardo et al., 2002), but does reduce activity levels in response to very low ambient temperatures (DeNardo et al., 2002). Thus, it is possible that *B. schneideri* has become secondarily diurnal, shifting to a diurnal pattern in response to the low night-time temperatures that occur across its geographic range.

Frequency of movement of Namaqua Dwarf Adders was surprisingly invariant across seasons and mirrored the increase in the mean distance moved during these periods (Maritz and Alexander, 2012b). The only obvious pattern was that males moved more frequently during spring and were significantly more likely to be active than female snakes during this period. All of our observations of copulating Namaqua Dwarf Adders ($n = 4$ pairs) were made during this period, supporting the notion that increased male movement in spring is likely the result of mate-searching.

Namaqua Dwarf Adders maintained a high level of activity during winter. Snakes also continue to feed during winter months (Wessels and Maritz, 2009). While winter activity in snakes from sub-tropical and tropical latitudes is not uncommon (Greene, 1997), temperate species in southern Africa are generally thought to fast during the winter months (Phelps, 2010). *Bitis schneideri* may be atypical in this respect due to the relatively low seasonal climatic variation across its distribution.

Compared to congenerics, Namaqua Dwarf Adders move relatively frequently. Male *B. schneideri* move on a nearly daily basis during spring, and pooled data for females in spring, and males and females in all other seasons, showed that on average, snakes move slightly more often than every other day (59.8 ± 18.3% of days). This contrasts strongly with activity levels of large-bodied Gaboon Adders (*B. gabonica*) that move on approximately only 10% of days (Warner, 2009). Secor (1995) showed that Sidewinder Rattlesnakes (*Crotalus cerastes*), relatively small-bodied, arid-adapted viperids from North America, move 32% of days annually, with a maximum of 60% of days during their active season. However not all ambushing viperids exhibit low movement frequencies. Marshall et al. (2006) demonstrated that Eastern Massasaugas (*Sistrurus catenatus*), small new-world viperids, moved relatively frequently (≈76% of days). Although the metadata are currently limited, an emergent trend is for small viperids to move more frequently than large ones. This trend could be the result of a body size-mediated variation in the time taken for snakes to give up hunting at particular ambush sites, which could in turn be dependent on prey type or an allometric relationship of some physiological attribute.

In general, high levels of activity make an organism vulnerable to predation (Gerritsen and Strickler, 1977). Reduction in predation risk that results from a sedentary lifestyle may, in fact, be one of the drivers that has resulted in the evolution of ambush foraging. However, ambush foragers do need to move in order to find novel suitable ambush sites (Tsairi and Bouskila, 2004), appropriate thermal resources (Webb and Shine, 1998), to avoid being detected by olfactory-oriented predators and prey (Burghardt, 1990; Downes and Shine, 1998; Kats and Dill, 1998) or to seek mates (Duvall and Schuett, 1997; Jellen et al., 2007; Warner, 2009; Glaudas and Rodríguez-Robles, 2011). Of these various reasons to move, seeking appropriate thermal resources is the motivation that most obviously scales with body size; since small snakes heat and cool more quickly than large ones, they might be at higher risk of overheating in a given situation, and thus have to move more often.

The work presented here provides an important contribution to our knowledge of activity patterns in snakes, and makes use of a novel methodology that, potentially, has a wider application in similar studies. It also provides important insights to the ecology of *Bitis schneideri*, a previously poorly known species. Given the uncertain future facing the Succulent Karoo Biome, studies similar to ours, but focusing on an array of organisms, are likely to hold the key to effective management and conservation in the area.

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