

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

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ABSTRACT: Although estimates of survival and population density are available for several snake populations, most of these are for populations in northern temperate environments. Here we present the results of a 3-yr mark–recapture study for an African species, the Namaqua Dwarf Adder (*Bitis schneideri*). We estimated survival, recapture probability, and population density by marking 279 adders (121 males, 108 females, 50 juveniles) on two study sites along the Namaqualand coast of South Africa. We recaptured 54 individuals (27 males, 23 females, 4 juveniles), yielding absolute recapture rates of 20.4% and 17.9% at each site respectively. The adult sex ratio of our sample did not differ significantly from equality. We fitted eight models that included both individual-dependent and time-dependent covariates to our recapture data, and compared models using Akaike information criterion corrected for small samples. The best models included snout–vent length and search effort covariates. Mean (\pm SD) estimated monthly apparent survival was low (0.86 ± 0.11 and 0.86 ± 0.12), as were mean recapture likelihoods (0.06 ± 0.04 and 0.06 ± 0.01). Population density estimates were similar for the two sites ($7.52 \pm 3.62 \text{ ha}^{-1}$ and $8.31 \pm 7.38 \text{ ha}^{-1}$). Juvenile snakes exhibited higher survival than adult females, which, in turn, had higher survival than adult males. Juveniles had a lower recapture probability than adult males or females. The likelihood of an individual leaving the study area was 6.8% and 9.4% per month for the larger and smaller sites, respectively. On the basis of our measures of apparent survival and emigration, we estimate annual survival rates of 39% and 56% for the two sites respectively. Population characteristics of *B. schneideri* differ substantially from those of other viperids, highlighting the need for additional population studies of African snakes.

Key words: *Bitis schneideri*; Mark–recapture; Namaqua Dwarf Adder; Succulent Karoo

ROBUST estimates of population size calculated using mark–recapture techniques generally require large samples and relatively high recapture rates. For species that are cryptic and exhibit low detection probability, such as many snakes, these data are difficult to collect. Additionally, working in difficult-to-access or politically unstable areas makes fieldwork problematic. It is therefore not surprising that Africa, despite its remarkable snake diversity, remains underrepresented in the field of snake population ecology (Parker and Plummer, 1987; Shine et al., 1998; Bonnet et al., 2002). Moreover, recent analyses describing global declines in snake populations (Reading et al., 2010) highlight the importance of population-based studies, especially in regions where biodiversity loss remains poorly quantified.

Most of the theory governing snake ecology has been derived from information garnered from a few well-studied model species (Siegel et al., 1987). Geographically, there is a strong bias toward North America and Europe

(Shine et al., 1998). Although such studies have formed the basis for an increase in the use of snakes as ecological model organisms (Shine and Bonnet, 2000), there is little indication of whether they are representative of African species, especially given the phylogenetic distinctiveness of African snake lineages (Cadle, 1994). In fact, Janzen (1976) argues that snake abundance in Africa is generally lower than that found in the Americas and Australia, but this idea remains speculative.

Population characteristics such as abundance, density, and survival rate are essential in the development of an understanding of the autecology of an organism. Although population estimates are available for several species of snakes globally (Parker and Plummer, 1987), relatively few of these have been estimated using mark–recapture models (Koons et al., 2009). In Africa, the situation is confounded by the fact that very few species have been investigated. Madsen and Osterkamp (1982) analyzed mark–recapture data for a population of *Lycodomorphus bicolor* on Lake Tanganyika, whereas more recent work in West Africa

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has provided density estimates for a few large, forest-associated species such as *Bitis gabonica*, *Bitis nasicornis* (Luiselli, 2006), and *Dendroaspis jamesonii* (Luiselli et al., 2000). Given the geographic extent and diversity of Africa, studies of four species, restricted to particular biomes, are unlikely to be representative of snake populations across Africa.

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

MATERIALS AND METHODS

Bitis schneideri is an arid-adapted viperid that inhabits coastal Sandveld habitats along the west coast of southern Africa (Broadley, 1983; Branch, 1998). It is the smallest viperid, with adults averaging 200 mm snout–vent length (SVL) and not exceeding 254 mm SVL (Maritz and Alexander, 2011). Our unpublished field observations strongly support the assertion that it is an ambush predator and that prey consists mainly of small vertebrates, primarily lizards and frogs (Branch, 1998). The species is currently listed as vulnerable by the IUCN as a result of habitat degradation over much of its distribution (Branch, 1988; World Conservation Monitoring Centre, 1996).

Our study was conducted on the farm Noup, in the Northern Cape Province, South Africa (30°08'S, 17°12'E). The study site has been described elsewhere (Maritz and Scott, 2010; Maritz and Alexander, 2011, 2012). We searched for Namaqua Dwarf Adders at two localities: a 27-ha north site and a 16-ha south site. The sites were similar with regard to

topography and vegetation, differing only in area and distance from the coastline (0.8 km and 2.6 km). Surveys were conducted over 17 mo between September 2007 and March 2010. Search effort totaled 596 observer-h, and was biased toward summer months when Dwarf Adders are more active and more likely to be encountered. All individuals were captured by hand and marked by clipping a unique sequence of ventral scales (Fitch, 1987). For each snake, we measured mass (to the nearest 0.1 g) using a digital balance, SVL (to the nearest 1.0 mm) using a ruler, and sex (as either male, female, or juvenile) on the basis of male-biased tail dimorphism (males have much larger tails than females). Sex-based differences in tail length are not apparent in individuals smaller than 140 mm SVL and these were thus designated as juveniles (Maritz and Alexander, 2011). For each capture we recorded the geographic coordinates of the location (using a handheld global positioning system device, Garmin eTrex and datum WGS1984).

To provide more accurate estimates of population parameters, we included two covariates in our analyses: SVL was included as an individual-dependent continuous variable that ranged from 99 to 251 mm, and allowed us to test for age effects on survival and capture probability. Total search effort invested during each month was applied to certain models as a time-dependent covariate (effort), calculated as the total duration of all observations at a particular study site, during a particular capture occasion. We standardized this covariate so that it ranged between zero and one.

We fitted Cormack–Jolly–Seber models to recapture data from each site separately using the mark–recapture analysis package (MacDonald, 2010) in R (R Development Core Team, 2009). We started by fitting a fully parameterized model (i.e., $\phi_{[svl]} p_{[effort, svl]}$) to the capture histories from the two populations, and tested for goodness of fit using Hosmer–Lemeshow (Hosmer and Lemeshow, 2000) and Osius–Rojek (Osius and Rojek, 1992) goodness-of-fit statistics. We then fitted an additional seven reduced models (Table 1) and compared them using Akaike information criterion corrected for small samples (AICc;

TABLE 1.—Relative performance of eight candidate mark–recapture models. ϕ = survival; svl = snout–vent length; p = monthly capture probability; effort = sampling effort; AICc = Akaike’s information criterion for small samples. Variables included in parentheses after parameters, (.) denotes that parameter was kept constant.

Model	No. parameters	North site			South site		
		AICc	Δ AICc	AICc weight	AICc	Δ AICc	AICc weight
$\Phi(\text{svl})\mathcal{P}(\text{svl}, \text{effort})$	4	314.30	0.00	0.41	197.85	0.00	0.28
$\Phi(\text{svl})\mathcal{P}(\text{effort})$	4	318.02	3.72	0.06	198.69	0.84	0.18
$\Phi(\text{svl})\mathcal{P}(\text{svl})$	3	330.36	16.06	0.00	198.86	1.02	0.17
$\Phi(\text{svl})\mathcal{P}(\cdot)$	3	333.80	19.50	0.00	199.80	1.95	0.10
$\Phi(\cdot)\mathcal{P}(\text{svl}, \text{effort})$	4	314.32	0.02	0.41	201.56	3.71	0.04
$\Phi(\cdot)\mathcal{P}(\text{effort})$	3	316.89	2.59	0.11	199.45	1.60	0.13
$\Phi(\cdot)\mathcal{P}(\text{svl})$	3	330.37	16.07	0.00	202.63	4.79	0.03
$\Phi(\cdot)\mathcal{P}(\cdot)$	2	332.70	18.40	0.00	200.55	2.70	0.07

Burnham and Anderson, 2002). To account for variation in model outputs we averaged all model estimates for ϕ , p , and N and weighted the contribution of each model using AICc weight scores.

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

Apparent mortality ($1 - \phi$) comprises those animals that do not survive to the next sampling occasion, as well as those that emigrate from the study site. The relative contribution of emigration to estimates of apparent mortality have been poorly investigated for most snakes (Parker and Plummer, 1987) but remains important in understanding overall survival. We attempted to apportion apparent mortality by simulating the relative contributions of emigration and mortality. To estimate the likelihood of an individual having emigrated from our study sites after 30 d (i.e., the likelihood that an animal initially detected on the study site will be absent during the following sampling occasion), we produced a random walk simulation in Microsoft Excel in which 1000 individuals were distributed randomly within an appropriately sized rectangular plot, and allowed to move independently in a stepwise manner. Data collected from radiotelemetered individuals (Maritz and Alexander, 2012) suggested no directional biases in movements, allowing us to model

movements with random turning angles. Model movements were based on mean daily step lengths of 3.2 ± 4.8 m d⁻¹ (Maritz and Alexander, 2012). Although the estimate of daily displacement underrepresents the movement of male snakes during spring, our radiotelemetry work (Maritz and Alexander, 2012) suggests that male snakes return to a smaller central portion of their home ranges after mate-searching forays. Thus, increased spring movements of males are unlikely to have a significant impact on our estimate of emigration. For the simulation we assumed that juveniles and adults experience similar rates of mortality and emigration likelihood. Although this is unlikely to be the case, our objective was to simulate emigration for the population as a whole that would predominantly comprise adults. We ran each cohort of 1000 individuals 10 times for each study site, and calculated mean (\pm SD) likelihood of emigration.

RESULTS

Search effort totaled 346 and 250 observer-h on the north and south sites, respectively. In total, we captured 279 snakes, comprising 121 males, 108 females, and 50 juveniles. Of these, 162 snakes (70 males, 67 females, and 25 juveniles) were captured at the north site, and 117 individuals (51 males, 41 females, and 25 juveniles) were captured at the south site. Twenty-seven individuals (13 males, 11 females, and 3 juveniles) from the north site were recaptured once, and six individuals (two males and four females) were recaptured twice. Nineteen individuals (10 males, 8 females, and 1 juvenile) from the south site were recaptured once, and two males were

TABLE 2.—Model-averaged estimates of population parameters estimated for *Bitis schneideri* at two study sites in South Africa. ϕ = survival; p = monthly capture probability; N = number of individuals at site; D = population density (ha^{-1}).

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

recaptured twice. Absolute recapture rates from the north and south sites did not differ from one another ($\chi^2 = 0.016$, $P = 0.68$), returning 20.4% and 17.9% of all marked animals respectively. The adult sex ratio for captured adult snakes was 1:1.12 (female:male), which was not significantly different from unity ($\chi^2 = 0.74$, $P = 0.39$).

Goodness-of-fit tests of our most parameterized model at each site provided no indication of a lack of fit at either the north site ($Z = 1411.19$, $P = 0.99$; $H = 3.13$, $P = 0.37$) or south site ($Z = 1032.81$, $P = 0.58$; $H = 4.75$, $P = 0.19$), which allowed us to continue to work with our suite of reduced models.

At both sites, the saturated model ($\phi_{[\text{svl}]}$ $p_{[\text{svl}, \text{effort}]}$) performed best (i.e., attained the lowest AICc score; Table 1). However, several other models scored similar AICc values: one model at the north site and four models at the south site attained ΔAICc scores of less than two. We chose the saturated model from the candidate models at both sites on the basis of their relatively low AICc scores, and for the sake of congruence in models across our study sites. At both sites, the saturated model suggested minor influences of SVL on either survival or recapture probability. Search effort was positively associated with capture probability at both sites.

Averaged estimates of ϕ and p were very similar for the two sites (Table 2). Because of differences in site area, the north site produced larger estimates of N than the south site. However, area-corrected density estimates for the two sites were similar (Table 2). Assuming that survival is fixed through the course of a year, our apparent monthly survival estimate of 0.86 translates into an annual apparent survival estimate of 0.19.

Apparent monthly survival differed significantly among adult males, adult females, and

juveniles ($F_{2,275} = 116.34$; $P < 0.001$), with juvenile snakes (0.93 ± 0.0063) exhibiting significantly higher (mean \pm SE) survival than adult females (0.84 ± 0.0049), which in turn exhibited significantly higher survival than adult males (0.82 ± 0.0046). Recapture probability also varied significantly among adult males, adult females, and juveniles ($F_{2,275} = 295.11$; $P < 0.001$); however, this significant effect was a result of juvenile snakes exhibiting significantly lower (0.036 ± 0.0011) recapture likelihood than adult males (0.066 ± 0.00082) and females (0.064 ± 0.00078).

The area of each site influenced likelihood of emigration from that site. At the larger north site, mean (\pm SD) likelihood of emigration after 30 d was estimated to be 6.8% ($\pm 0.5\%$), which was lower than the mean estimated likelihood of emigration for the south site, 9.4% ($\pm 1.0\%$). Using these estimates of emigration likelihood increases the estimated mean monthly survival to 0.92 and 0.95 for the north and south sites, respectively, and these translate into annual survival estimates of 0.39 and 0.56, respectively.

DISCUSSION

Our findings represent one of the first robust, empirical assessments of the survival rate, capture probability, and population density of any African snake. *Bitis schneideri* study populations in coastal Namaqualand did not exhibit a biased sex ratio, experienced low apparent survival rates, and occurred at relatively high population densities. Additionally, juvenile snakes exhibited relatively high apparent survival and relatively low recapture probabilities compared with adults. Adult males exhibited significantly lower apparent survival than adult females, but similar recapture probabilities. Finally, emigration may account for less than 10% of apparent

mortality. The general congruence among model outputs for the two populations studied support our findings. In general, capture rates were low, and as a result many of the parameters that we have estimated are associated with wide confidence limits. However, such problems are unavoidable for cryptic organisms such as many snake species (Turner, 1977; Parker and Plummer, 1987).

Studies of African snake population dynamics are rare, making direct comparison of our result with other African species difficult. To our knowledge, no other estimates of survival exist for an African snake population. Numerous studies on primarily European and North American populations suggest that (apparent) survival varies widely among snake species (0.35–0.85; Shine and Charnov, 1992). More recently, several mark-recapture modeling analyses of snake populations have reported survival estimates for viperids including *Vipera aspis* (0.75; Flatt et al., 1997), *Crotalus oreganus* (0.55–0.82; Diller and Wallace, 2002), *Crotalus horridus* (0.82–0.95; Brown et al., 2007), and *Agkistrodon piscivorus* (0.79; Koons et al., 2009); colubrids including *Thamnophis radix* (0.35–0.45; Stanford and King, 2004) and *Thamnophis atratus* (0.56–0.64; Lind et al., 2005); and elapids including *Hoplocephalus bungaroides* (0.82; Webb et al., 2003) and *Rhinoplocephalus nigrescens* (0.74; Webb et al., 2003).

Our estimates of survival for *B. schneideri* (0.39–0.56) are low in comparison with several of the estimates cited above, especially in comparison with measures for other viperids. Shine and Charnov (1992) demonstrated a strong relationship between mean annual survival and age at maturity for snakes, with rapidly maturing species exhibiting lower annual survival rates. Maritz and Alexander (2011) show that sexual maturity is reached at the age of 10–15 mo in *B. schneideri*. This rapid maturation and the low survival reported here fit the trend described by Shine and Charnov (1992).

Our finding that juvenile *B. schneideri* have higher survival rates than do adults may be the first corroborating evidence of the prediction of Pike et al. (2008) that juvenile snakes exhibit behavioral traits that reduce predation risk. In many ambush-foraging species (such as *B.*

schneideri and other ambush-foraging snakes), bouts of movement are likely to pose an increased predation risk (Bonnet et al., 1999). Given that mate-searching movements appear to be the chief motivation for movement in this species (Maritz and Alexander, 2012) and that juvenile snakes do not mate-search, then juvenile snakes may face greatly reduced predation risk and thus higher survival. This idea is supported by our concurrent estimates of recapture probability that are relatively low (see below), and relatively low measures of daily displacement by juvenile snakes (Maritz and Alexander, 2012).

We calculated a mean recapture probability of $\approx 6\%$ for our study population. Recapture probability was low compared with those estimated for other snake populations (Diller and Wallace, 2002; Lind et al., 2005; Brown et al., 2007), was strongly influenced by search effort, but weakly influenced by SVL. We detected no difference in recapture probability of adult males and females, despite males moving much farther than female snakes during the spring mate-searching season (Maritz and Alexander, 2012). This finding supports the hypothesis that outside of the brief mate-searching season, male and female snakes exhibited similar behavioral repertoires. Mean (\pm SE) juvenile recapture likelihood was low (3.6%), supporting our hypothesis of reduced movement during this life phase.

Density estimates for African snake populations are also rare, making generalizations regarding African snake populations difficult. Luiselli (2006) estimated that both *B. gabonica* (0.16 ha^{-1}) and *B. nasicornis* (0.10 ha^{-1}) occurred at much lower densities than our measures for *B. schneideri*. Additionally, *D. jamesonii*, a large elapid snake, is reported to occur at low population densities (0.11 ha^{-1} ; Luiselli et al., 2000). Conversely, the aquatic *L. bicolor* is reported to occur at densities of up to 380 ha^{-1} (Madsen and Ostercamp, 1982), but this measure may be inflated by snakes being attracted to a focal feeding point. Parker and Plummer (1987) reviewed snake population densities, and found that estimates of population density ranged from $<1 \text{ ha}^{-1}$ (including the viperids *Crotalus cerastes*, *C. horridus*, and *C. oreganus*) to $>1000 \text{ ha}^{-1}$

(*Diadophis punctatus* and *Regina alleni*). However, not all of the estimates reported by Parker and Plummer (1987) are the result of robust mark–recapture analyses, and few are the result of models that simultaneously include estimates of recapture probability (e.g., Koons et al., 2009). Generally, viperid populations do not occur at densities $>10 \text{ ha}^{-1}$ (Parker and Plummer, 1987). Two noteworthy exceptions are the island endemics *Gloydius shedaoensis* ($\approx 273 \text{ ha}^{-1}$; Sun et al., 2001) and *Bothrops insularis* ($\approx 55 \text{ ha}^{-1}$; Martins et al., 2008). Although *Bitis schneideri* populations do not reach such extremes, our measures (7.52 ha^{-1} and 8.31 ha^{-1}) are still high compared with most viperid populations. Peters and Wassenberg (1983) demonstrated that for most groups of animals, smaller-bodied species tend to occur at higher densities. Although this pattern has not been unequivocally demonstrated for snakes (Luiselli et al., 2005), our relatively high population density estimates for *B. schneideri* are concordant with this generalization.

Partitioning the contributions of mortality and emigration on apparent mortality is problematic, and remains a major challenge facing mark–recapture analysis. Our analysis represents a first attempt at understanding these relative contributions. Most studies report apparent survival, as we have, but with little or no discussion of the contribution of emigration. Our random-walk model showed that in the short term, emigration from the study site by a marked individual was relatively low ($<10\%$). *Bitis schneideri* are relatively sedentary animals, occupying small home ranges (Maritz and Alexander, 2012). Given the size of our study sites and the sedentary nature of our study animals, the likelihood of a marked individual emigrating from the study site is dependent upon the initial capture location of the animal. Accordingly, estimates of emigration are probably more sensitive to study-plot size and shape than to the duration of the study, because increased duration gives the snakes the time to emigrate, but also gives them time to return to the plot. We therefore surmise that our estimates for a 30-d sampling occasion provide an appropriate estimate of emigration likelihood.

If viewed as a proportion of apparent mortality, our simulations suggest that emigration could have important implications for the interpretation of survival. Our estimates of emigration show that it could make up 49% of apparent monthly mortality at the north site and 67% at the south site due to the difference in size of the sites. This finding also has important implications for other studies that have not factored emigration out of apparent survival measures. However, our emigration-corrected measures of monthly and annual survival are relatively low, and do not change the interpretation that our study system experiences high mortality. Parker and Plummer (1987) summarized the population traits of snakes, and described early-maturing temperate colubrids (low adult survivorship, low longevity, annual reproduction, high fecundity). *Bitis schneideri* is more closely allied with these early-maturing colubrids than the late-maturing viperids of temperate regions.

Our study represents one of very few studies that have empirically assessed population parameters for an African snake population. We have demonstrated that *B. schneideri* exhibits low recapture probability, high mortality rates, and relatively high population densities. The development of generalized theories that appropriately describe African snake ecology will require the study of additional African species. Until this situation is remedied, management actions related to African snake populations will remain speculative at best.

Acknowledgments.—We thank E. Oppenheimer and Son, the Rufford Small Grants Foundation, and the South African National Biodiversity Institute for financial support. The Wessels family and numerous fieldworkers provided valued logistic support. S. Nielsen provided valuable comments on this manuscript. All work was cleared under Northern Cape Province Department of Tourism, Environment and Conservation (0914/07 and FAUNA 698/2009) and University of the Witwatersrand Animal Ethics Screening Committee (2007/68/1 and 2007/69/3) permits. Two reviewers improved an earlier version of this manuscript.

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Accepted: 3 January 2012
Associate Editor: Rulon Clark