

# Namaqua dwarf adders must breed frequently: the problem with being small

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## Keywords

*Bitis schneideri*; succulent karoo; low frequency of reproduction; Africa.

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Editor: Virginia Hayssen

Received 6 March 2012; revised 26 June 2012; accepted 12 July 2012

doi:10.1111/j.1469-7998.2012.00957.x

## Abstract

Reproductive frequency is a key component of reproductive output, and has important influences on organismal fitness and population persistence. Viperid snakes, like many other ectothermic vertebrates, generally exhibit a low frequency of reproduction (LFR), as females only reproduce every second year, or even less frequently. However, for small-bodied species with constrained clutch/litter sizes, and low survival, reproductive frequency cannot be too infrequent if populations are to persist. We assessed whether *Bitis schneideri*, a small, arid-adapted viperid snake from southern Africa has the LFR typical of many other viperids, despite having low survival and small litters. We calculated the reproductive frequency required to sustain a population using information gathered from recent studies of the ecology of the species. The small litter size imposed by being small-bodied, and low annual survival, require *B. schneideri* to reproduce frequently, probably annually, for populations to persist. We also assessed the reproductive status of all available preserved adult females. A high proportion were reproductive (up to 80% during summer), with developing or mature follicles, or developing young. Such frequent reproduction is atypical, even among closely related species, and might be facilitated through the capacity of *B. schneideri* to feed year-round in the aseasonal habitat in which it occurs. We predict that future studies of small-bodied species from climates that allow for extended periods of feeding will continue to show that frequent reproduction is more widespread among vipers than is currently assumed.

## Introduction

Reproductive frequency (the number of clutches/litters produced by a female organism annually) is a fundamental component of reproduction. Not only does it contribute to total lifetime reproductive output and ultimately the fitness of an organism, but it governs the number of young entering a population over time and thus, ultimately, the viability of the population. Low frequency of reproduction (LFR; Bull & Shine, 1979) occurs when individuals reproduce every other year, or even less frequently. The condition is widespread among ectothermic vertebrates (Bull & Shine, 1979) and is particularly common among viviparous viperid snakes with females of many species breeding only every 2 or 3 years (Blem, 1982; Seigel & Ford, 1987; Shine *et al.*, 1998; Shine, 2003). LFR has important population effects as it limits the number of young entering a population, posing a challenge to population persistence.

For a population of equal sex ratio to persist, on average, each female needs to produce only two surviving young in her lifetime (Cole, 1954; Stearns, 1976). Following this principle, Pike *et al.* (2008) produced a model that relates mean annual reproductive frequency ( $n$ ), age at first reproduction ( $a$ ), mean

clutch/litter size ( $c$ ), and adult ( $S_A$ ) and juvenile ( $S_J$ ) survival rates. Pike *et al.* (2008) used the model to estimate juvenile survival rates of reptiles by substituting known values of  $n$ ,  $a$ ,  $c$  and  $S_A$ . However, the model can also be used to estimate mean annual reproductive frequency from other known life history variables if those measures are available. Moreover, the model illustrates how mean annual reproductive frequency mediates the trade-off between survival and litter size.

Various traits allow vipers to overcome the population effects of LFR. Some infrequently reproducing species have large litters (maximize  $c$ ). Puff adders (*Bitis arietans*) are large-bodied vipers that can produce litters of up to 156 young (Branch, 1998). Other species maximize  $S_J$  by producing well-developed young that have higher survival, or are long-lived as adults (high  $S_A$ ). Timber rattlesnakes (*Crotalus horridus*) provide a well-studied example of this strategy, living as long as 35 years and producing litters of 6–14 individuals (Gibbons, 1972; Brown, 1991; Martin, 1993, 2002).

*Bitis schneideri* is an arid-adapted viperid that inhabits coastal dunes along the west coast of southern Africa (Broadley, 1983; Branch, 1998). Climatic conditions within the geographic distribution of the species are relatively aseasonal, a result of the moderating effect of the Benguela Current

(Desmet, 2007). Reproductive frequency in *B. schneideri* is interesting because the species is small-bodied (it is the smallest viper; Maritz & Alexander, 2011) and produces litters of 2–7 young (low  $c$ ; Haacke, 1975; Broadley, 1983; Branch, 1998) but also shows low rates of adult and juvenile survival (low  $S_A$  and  $S_J$ ; Maritz and Alexander, 2012a). We hypothesize that because of these demographic traits, reproductive frequency in *B. schneideri* is more frequent than the LRF seen in many other vipers, including several congeners.

Reproductive frequency is often measured as the proportion of reproductive females in a sample of museum specimens (Seigel & Ford, 1987). However, *B. schneideri* is poorly represented in museum collections (fewer than a total of 30 females specimens in all major southern African collections) making adequate assessment of reproductive frequency through the dissection of preserved material challenging. We thus investigated reproductive frequency in *B. schneideri* using both approaches described above. Firstly, we derived measures of reproductive frequency based on the formula presented in Pike *et al.* (2008) using our existing estimates of litter size, survival, and age to maturity. We then tested the validity of the predicted reproductive frequency by examining the reproductive condition of the available preserved specimens.

## Materials and methods

We rearranged formula 4 from Pike *et al.* (2008) to make mean annual reproductive frequency ( $n$ ) a function of mean clutch size ( $c$ ), juvenile survival ( $S_J$ ), adult survival ( $S_A$ ) and age at first reproduction ( $a$ ) so that:

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

The model relies on the assumption that the study population is stable. Maritz and Alexander (2012a) modelled population density of two South African populations of *B. schneideri* over a 3-year period using mark-recapture analysis. Using those data and the most parsimonious Cormack–Jolly–Seber model (for details see Maritz & Alexander, 2012a) we estimated population size ( $N$ ) during each month of study. We detected no significant change in  $N$  over the study period in either population ( $F_{1,14} \leq 2.40$ ;  $P \geq 0.14$ ).

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

### Survival rates (adult and juvenile)

Maritz & Alexander (2012a) derived annual survival estimates for adult *B. schneideri* from two populations (39 and 56%) using mark-recapture analysis. We calculated the reproductive frequency required to sustain a population using survival rates ranging from 35 to 60%, encompassing the range of likely survival rates for adult snakes at our study site.

Maritz & Alexander (2012a) demonstrated that juvenile survival was likely to be higher than adult survival. We thus varied annual juvenile survival between 39 and 66% in our

model (set to be  $1.1 \times$  adult survival-based modelled rates reported in Maritz & Alexander, 2012a).

### Litter size

The reported litter size of *B. schneideri* ranges between two and seven (Haacke, 1975; Broadley, 1983; Branch, 1998). We calculated a mean ( $\pm$  standard deviation) litter size of  $c = 3.6$  ( $\pm 1.0$ ) offspring based on our analysis of 13 preserved gravid females (see Dissection of preserved material). We tested for sensitivity of our analysis by estimating reproductive frequency required to maintain a population for mean clutches of between three and four offspring per litter.

### Age at first reproduction

Female *B. schneideri* grow rapidly and reach sexual maturity at approximately 15 months of age (Maritz & Alexander, 2011) suggesting that a female could reproduce during her second spring. Based on our observations of free-ranging snakes, we assumed mating to be seasonal, taking place in October, with females producing young the following February.

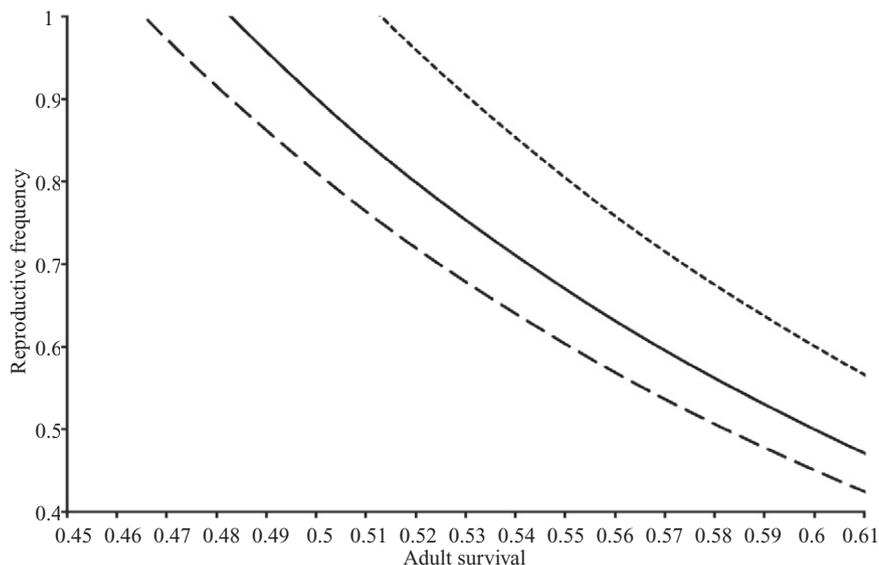
### Dissection of preserved material

We dissected 16 adult female snakes in the collection of the Ditsong National Museum of Natural History (formerly the Transvaal Museum). Additionally, we encountered six adult female snakes that had been killed by motor vehicles. Road-killed specimens might, potentially, not be representative of the population as reproductive snakes might have modified behavioural repertoires. However, our data revealed no change in mean daily displacement made by females in various seasons (Maritz & Alexander, 2012b). We examined all adult females for the presence of vitellogenic follicles and developing young. Another potential source of bias can result if the dissected snakes in the sample have smaller or larger body size relatively to the population of adult females (Blem, 1982). We tested for this effect by comparing the mean body length of the dissected snakes with the known body length distribution of a wild population reported in Maritz & Alexander (2011), using a Sign Test.

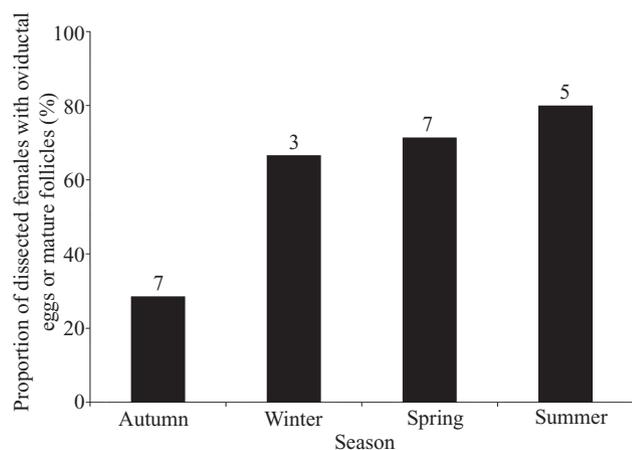
## Results

The reproductive frequency required to maintain a stable population was strongly dependent on  $c$  and  $S_A$ , and ranged between 0.45 and 2.87 litters  $\text{yr}^{-1}$ . However, for our best estimates of these variables ( $c \approx 3.6$  offspring litter $^{-1}$ ;  $S_A \approx 48\%$ ) the model predicted that the mean annual reproductive frequency required to maintain a stable population was  $\approx 1$  litter  $\text{yr}^{-1}$  (Fig. 1). We therefore expected a very high proportion of preserved adult females to be reproductive (i.e. to either have oviductal eggs or mature follicles).

In total we dissected 22 adult female snakes. Seven of these were preserved during the austral autumn (March–May), three during winter (June–August), seven during spring



**Figure 1** Mean annual reproductive frequency ( $n$ ) of *Bitis schneideri* as a function of annual adult survival rate ( $S_A$ : x-axis) and mean litter size ( $c$ : short dashes;  $c = 3$ ; solid line;  $c = 3.6$ ; long dashes:  $c = 4$ ). X-axis range limited to values of  $S_A$  that require  $n \leq 1$ .



**Figure 2** Proportion of dissected adult female *Bitis schneideri* that contained oviductal eggs or mature follicles in autumn (March–May), winter (June–August), spring (September–November) and summer (December–February) respectively. Values represent sample size.

(September–November) and five during summer (December–February). The size distribution of the dissected snakes did not differ from that of a sample of 96 adult females reported by Maritz & Alexander (2011) ( $Z = 1.31$ ;  $P = 0.19$ ). A very high proportion of adult females were reproductively active (Fig. 2). During summer 80% of snakes contained mature follicles or large oviductal eggs.

### Discussion

Our prediction of reproductive frequency and the subsequent examination of museum specimens strongly support the idea that *B. schneideri* breeds frequently, with most adult females reproducing annually. Annual reproduction is apparently

unknown among viviparous African viperids (Phelps, 2010) and is seemingly rare among vipers in general (Seigel & Ford, 1987).

Reproduction is a relatively well-investigated aspect of snake ecology, and continues to grow as research on historically under-represented taxa proliferate (Shine, 2003). However, the ecology of species inhabiting the developing world, including most African species, remains largely enigmatic. As more species are investigated, it is likely that the theory governing our understanding snake ecology will be challenged. For example, the LFR that is currently thought to characterize viperid snakes might be an artefact of studies being biased towards viviparous, large-bodied, rodent-eating species typical of northern temperate habitats (Ineich *et al.*, 2006). If this is in fact the case, frequent reproduction in vipers might be more widespread than currently understood.

Numerous authors have recognized the role of energy intake in the modulation of reproductive cycles of snakes in general, and specifically in vipers (Andren & Nilson, 1983; Shine & Madsen, 1997; Madsen & Shine, 1999, 2000; Shine, 2003). Aldridge (1979) stated that most temperate-zone species are probably capable of annual reproduction, and that LFR is the result of low energy intake associated with low foraging success or short feeding seasons. It is thus unsurprising that many of the species that are characterized by LFR are known to reproduce annually in certain situations such as warmer parts of their geographic distributions or in years with abundant food (Seigel & Ford, 1987; Madsen & Shine, 1992; Beaupre, 1995; Zuffi, Giudici & Iolà, 1999; Hill & Beaupre, 2008).

If frequently reproducing viperids require a high energy intake, species whose persistence depends on frequent reproduction, such as small-bodied species, should only occur in areas where environmental conditions facilitate adequate feeding. This might occur where food is locally abundant or where conditions allow an extended season for feeding and

digestion. Female *B. schneideri* appear to be able to breed frequently due to year-round feeding (Wessels & Maritz, 2009; Maritz, 2011) which results from moderating climatic effect of the Benguela Current off the west coast of southern Africa. This moderating effect occurs along the coastal parts of the west coast over an area corresponding to the geographic distribution of the species. It is thus plausible that the species is limited to areas that allow for frequent reproduction, providing a proximal range limiter for the species.

Our analysis (Fig. 1) demonstrates that biennial reproduction is possible in *B. schneideri* ( $n < 0.6$  litters yr<sup>-1</sup>). However, for a population to persist for extended periods of time under these conditions, the population needs to concurrently experience survival rates that are higher than we have measured (Maritz & Alexander, 2012a). Thus, periods of reduced frequency of reproduction resulting from reduced prey availability can only be sustained if there is a concomitant increase in survival.

Small-bodied species are often constrained in the number of offspring that they can produce (Shine, 1992). If individuals of these species also experience low survival rates, then frequent reproduction is not simply a situational response to resources, but also a requirement for population persistence. Our data indicate that this is the case in *B. schneideri*. Interestingly, the small-bodied *Vipera kaznakovi* is also known to produce small litters (3–5 offspring litter<sup>-1</sup>; Phelps, 2010) and is reported to breed annually (Orlov & Tuniyev, 1990). We predict that similarly high reproductive frequencies will be discovered in other small-bodied vipers.

The body of literature describing the ecology of snakes is biased towards high-latitude temperate forms and might be inappropriate for a large portion of species. Studies of small-bodied viperids, particularly those from non-temperate areas are necessary to accurately ascertain how widespread the phenomenon of high reproductive frequency is among viperids. Studies such as ours are essential for uncovering patterns that as yet have not been described in the literature biased towards North American and European fauna.

## Acknowledgements

We thank E. Oppenheimer and Son, the Rufford Small Grants Foundation and the South African National Biodiversity Institute for financial support. Ditsong National Museum of Natural History permitted access to the specimens in their collection. 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. Three reviewers improved an earlier version of this manuscript.

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