Prey excavation by *Psammophylax rhombeatus rhombeatus* (Colubridae: Psammophiinae) from South Africa

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PSAMMOPHIINES represent a well-defined monophyletic radiation of African, west Asian, and Mediterranean snakes comprising eight genera and approximately 45 species (Branch, 1998; Kelly *et al.*, 2003; Kelly, 2005; Shine *et al.*, 2006). Most snakes of this clade exemplify the classic convergent "whipsnake" morphology and behaviour (Shine *et al.*, 2006). They are alert, fast-moving, diurnal predators that are able to exploit a diverse array of prey classes (Baha el Din, 1998; Akani *et al.*, 2003; Shine *et al.*, 2006). Despite their ubiquity and ecological importance throughout their range, there have been few field studies investigating the ecology of psammophiines.

It is widely believed that visual stimulation is among the most important cues for predation in diurnal terrestrial snakes, especially whipsnakes (Shine, 1980; Ota, 1986; Mori *et al.*, 1992; Luiselli, 2006). However, complex chemosensory behaviour exhibited by species in the Psammophiinae (De Haan, 2003; De Haan & Cluchier, 2006) suggests that members of this clade may rely on chemical cues in foraging more heavily than previously presumed. Here we report on the excavation of a visually-concealed prey species by the southern African psammophiine, *Psammophylax rhombeatus rhombeatus* (Rhombic Skaapsteker). Despite its wide range (most of South Africa, Lesotho, and Swaziland and disjunct populations in Namibia; Branch, 1998) and local abundance, surprisingly little is known about its diet and foraging strategies. Two previous museum-based studies (Van Wyk, 1988; Flemming & Douglas, 1997) investigated the ecology of the Rhombic skaapsteker, but there have been no published field studies of the species. The following account documents a foraging strategy previously unknown in the psammophiine clade.

METHODS

Observations took place on 2nd November 2006 (South African spring) on Farm Steenboksfontein Nature Reserve (32°10'S, 18°18'E), approximately 7 km south of Lambert's Bay on the semi-arid coast of the Western Cape Province of South Africa, during a radiotelemetric study of *Psammophylax r. rhombeatus*. Annual rainfall in this region ranges from 50–300 mm, with approximately 80% of the precipitation occurring between April and September (Lovegrove, 2003). This Mediterranean-type climate provides the conditions for strandveld (open scrubland) vegetation characterized by woody species that occur on sandy, calcareous soil on low lying coastal plains (Manning & Goldblatt, 2000).

Implantation of radiotransmitters (Holohil, SB-2) followed the procedures of Reinert and Cundall (1982). Snakes were relocated using a hand-held, 3-element Yagi antenna and CE-12 receiver (Custom Electronics, Urbana, Illinois). Photo documentation and short video clips of the excavation behaviour were taken using a MVC-CD1000 Sony Digital Still Camera.

RESULTS

The focal skaapsteker (adult male, weight: 59.2 g, SVL: 49.2 cm, TL: 15.7 cm) was located at 13:32 h on 2nd November 2006 (ambient temperature: 25.4°C; soil temperature: 23°C; humidity: 56%) by radiotelemetry on open sand where it was observed using its head and neck to dig sand out of a deep burrow (Fig. 1A). The dimensions of the hole (approximately 10 cm in diameter) suggest it had been originally excavated by a mammal; moreover, the amount of sand the snake was able to displace with each scooping action was minimal (less than 5 cm^3) and could not have created the resulting burrow in any short period of time.

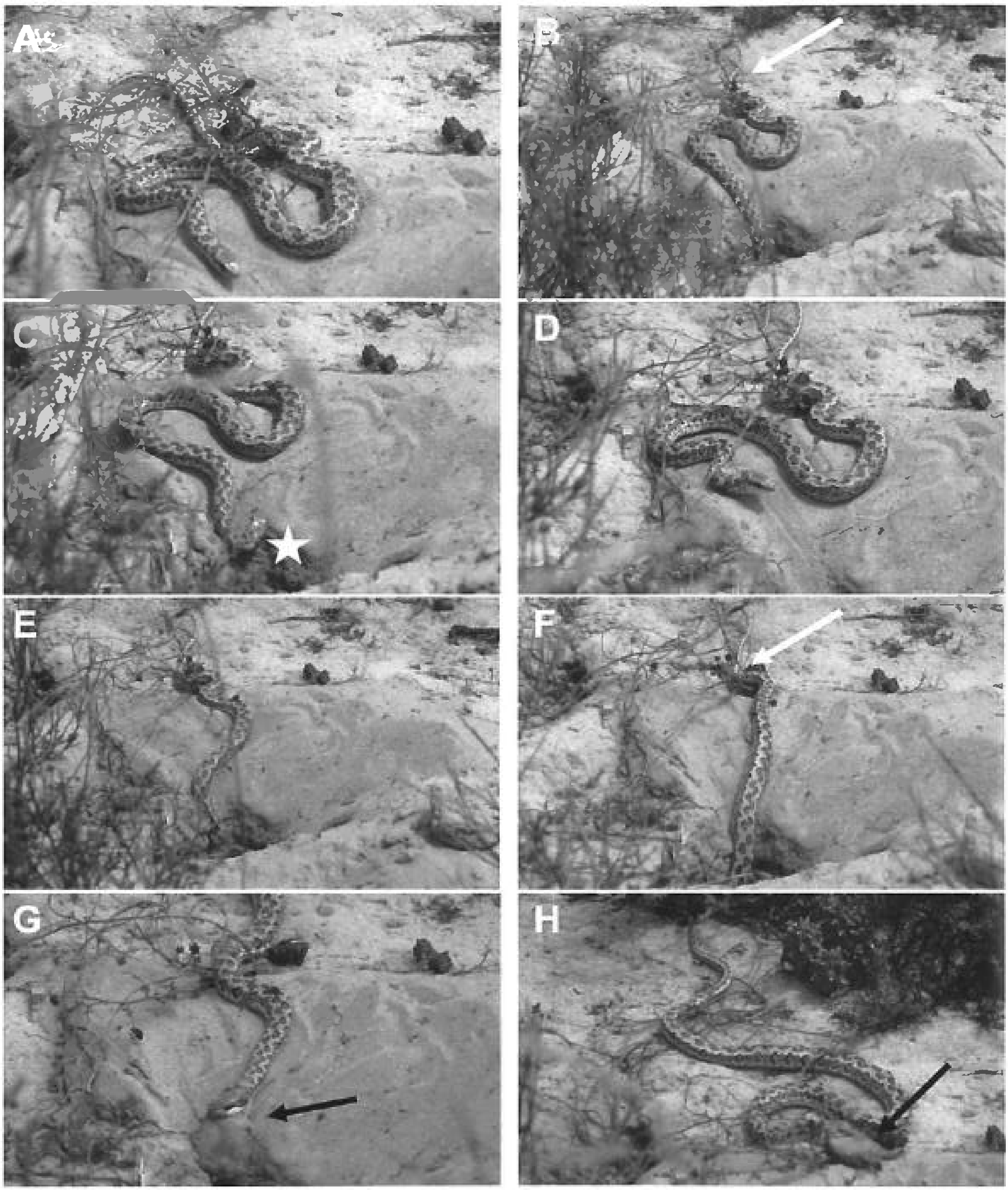

Figure 1. *Psammophylax r. rhombeatus* excavating *Breviceps namaquensis.* (A) Snake when first located at 13:32 h. (B) Snake descending into the burrow head-first. White arrow shows the anchorage point used by the snake when descending into burrow. (C) Snake emerging from burrow and using the bent neck to scoop out sand (white star). (D) Snake emergent during period of rapid excavation (3–5 scoops per 15 sec interval). The displaced whorls of sand around the snake are indicative of body movements made during excavation. (E) Forebody extended into burrow during period of slow excavation prior to prey prehension. (F) Furthest subterranean extension of forebody facilitated by tail anchorage (white arrow) to achieve this. (G) Snake reversing out of burrow at 13:45 h dragging a large *Breviceps namaquensis* (black arrow). (H) Snake pausing to manipulate prey (black arrow) while reversing away from burrow.

The posterior part of the body and tail were anchored around a bush as the snake entered and exited the steep entrance to the burrow (Fig. 1A–F). The snake adjusted its grip around the vegetation as it cycled in and out of the burrow (see progression of Fig. 1A–F). Each time the forebody of the snake descended into the burrow it emerged using the crook of its neck to scoop sand from the burrow entrance (Fig. 1C). It switched between right and left flexures frequently and did not appear to favor one side over the other. It continued digging rigorously (3–5 scoops every 15 s) for approximately 7 min, pausing only occasionally.

The skaapsteker then changed its digging rate; spending longer time intervals (5–15 s) with its forebody beneath the surface (Fig. 1E–F). During these extended periods, the visible portion of its body began swaying from side to side, emerging occasionally to displace sand (although more sporadically and at a slower pace than previously). After a prolonged period (25 consecutive seconds) of having the anterior half of its body below ground, the snake slowly began to reverse out of the hole, still using its tail as anchorage. At 13:45h it emerged with a Namaqua rain frog (*Breviceps namaquensis*) head-first in its mouth (Fig. 1G–H). Based on known measurements of the focal snake, the frog was approximately 5 cm in length and at least 3 cm in width.

The skaapsteker reversed entirely out of the steep burrow but paused four times to advance the frog further into its mouth. Once completely out of the burrow the snake continued to reverse over an additional ~20 cm of level surface (Fig. 1H). It then traveled forward to a bush less than a meter from the hole, where it began a series of lateral head and neck undulations until the entire body of the frog had been ingested. After the bulge had progressed to the stomach, the snake briefly remained laid out straight and motionless and finally moved to another bush about 2 m west of the excavated burrow (14:01 h). Throughout excavation and ingestion the skaapsteker appeared unaffected by observer proximity (~ 1.5 m) and movement.

DISCUSSION

Van Wyk (1988) investigated feeding habits of *Psammophylax r. rhombeatus* using preserved museum specimens and found that small mammals comprised 82% of the identifiable prey items. However, his study was geographically limited to a small area of the species' range and its results may not be representative of the species as a whole, as other sources list frogs as a dominant prey category (Broadley, 1977; Jacobsen, 2005). Our more comprehensive dietary data show that nocturnal and/or diurnally subterranean prey comprise a considerable proportion of the diet of *P. r. rhombeatus* (Cottone & Bauer, unpublished data). Other information concerning the diet of this species is based on anecdotal dietary notes (Broadley, 1983; Branch & Bauer, 1995) and in all of these cases foraging strategy can only be inferred from prey type.

Breviceps namaquensis is a nocturnal, burrowing frog that only emerges from its burrow during rainy periods (Passmore & Carruthers, 1995). Because a night of rain preceded the described predation event, it is likely that the skaapsteker detected the prey the next day using chemical cues. Presumably the snake had only to dig out an entrance plug in order to access the frog, since the burrow itself appeared to have been originally excavated by a mammal. Based on previously published records, as well as 19 identifiable anurans extracted from the stomachs of preserved skaapstekers in our broader study, this is the only *Breviceps* dietary record for *P. r. rhombeatus*.

Digging behaviour similar to that documented here has been reported in colubrid snakes of other lineages. For example, *Pituophis catenifer sayi*, *P. c. affinis*, and *P. melanoleucas mugitus* have been recorded digging through loose sand using neck scooping actions similar to that of *P. r. rhombeatus* in order to retrieve subterranean pocket gophers (*Geomys*) (Carpenter, 1982; O'Brien *et al.*, 2001). Carpenter (1982) also used laboratory data to suggest that *Pituophis* uses chemoreception to actively detect such buried prey.

Other terrestrial colubrid snakes also exploit subterranean prey through probable chemical detection and subsequent extraction. *Dinodon semicarinatum* has been recorded digging and feeding on sea turtle eggs and unemerged hatchlings (*Chelonia mydas* and *Caretta caretta*) (Mori *et al.*, 1999). The Australian whipsnake, *Demansia vestigiata*, has also been reported extracting a buried *Limnodynastes ornatus* (Trembath & Rowley, 2005). However, both these snakes excavated prey by pushing their snouts through the soil, a different technique than the shoveling motions used by *Pituophis* and *Psammophylax r. rhombeatus*. *Lampropeltis getula holbrooki* has likewise been documented excavating and eating turtle eggs (Brauman & Fiorillo, 1995), although details of the digging technique were not discussed.

In cases where the digging technique is known, the time spent excavating exposes the snake to prolonged predator vulnerability; however, subterranean prey are very unlikely to escape (Trembath & Rowley, 2005). So despite the high risk, either the pay-off of a guaranteed meal or a particularly rich food source may be sufficient for the strategy to be maintained. This could be advantageous for a wide foraging snake by decreasing its overall energy expenditure and exposure to predators.

Additionally, excavation can be beneficial for reasons other than prey capture. A second skaapsteker being tracked was observed for six minutes digging a depression in the sand using the same neck scooping behaviour noted above before it abandoned the excavation (perhaps disturbed by observer presence). This particular snake was observed basking in depressions similar in dimensions to the one it was witnessed excavating throughout the two month period it was being tracked, suggesting that skaapstekers also dig in order to thermoregulate and/or more effectively avoid detection while basking. This behaviour appears analogous to the "cratering" behaviour observed in *Crotalus cerastes cerastes* and other viperids (Brown & Lillywhite, 1992), although the depressions are formed through different body movements.

Our observations suggest that excavation behaviours in skaapstekers may be useful in multiple ecological contexts. Existing data suggest that *Breviceps* species are not crucial, or even common, components in skaapsteker diets, although excavation may also be required to obtain certain mammalian prey, as consumed by *Psammophylax* in the Free State province of South Africa (Van Wyk, 1988). Mechanical specializations, if any, for excavation, as well as the role of chemosensation in the location of subterranean prey have yet to be investigated in skaapstekers but may ultimately provide a functional context for the ecology of African psammophiines which, until now, has been investigated almost exclusively through museum-based dietary studies (Shine *et al.*, 2006).

ACKNOWLEDGEMENTS

We thank the Western Cape Conservation Board for supplying the permits to conduct research and Villanova University for funding the research. We would also like to thank Gerrit Burger for providing the accommodation and permission to conduct the study on his farm. Special thanks to Le Fras Mouton, Mandi Ablas, Hannes Van Wyk, Dahné DuToit, and Jeannie Hayward from Stellenbosch University for logistical help throughout the field season. Finally, thanks to Awesome Tony Gamble for providing the camera with which photo documentation during this study was taken. All snakes in this study were handled in accordance with IACUC standards (05–06) issued through Villanova University.

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