

Dietary Habits and Reproductive Biology of Typhlopid Snakes from Southern Africa

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ABSTRACT.—We studied diets, sexual dimorphism, and reproductive biology of six taxa of poorly known African blindsnakes (*Rhinotyphlops lalandei*, *Rana mucruso*, *Rana schlegelii petersii*, *Rana schlegelii schlegelii*, *Typhlops bibronii*, and *Typhlops fornasinii*) by dissection of 649 preserved museum specimens. Females matured at larger sizes than conspecific males, and the degree of sexual size dimorphism was most extreme in the large heavy-bodied *R. s. schlegelii*. Reproduction was highly seasonal in temperate-zone *T. bibronii* and *R. lalandei*, with vitellogenesis in spring, oviposition in late summer, and hatching in autumn. All species were oviparous, with mean clutch sizes of four to 25 eggs. Clutch sizes were strongly correlated with maternal body size in *T. bibronii* and *R. lalandei*. African *Rhinotyphlops* and *Typhlops* fed mainly on larvae and pupae of ants (88–97% of prey items for five of the six species), but adult termites were also eaten. Only *R. mucruso* fed on termites to a significant degree (38% of prey items). All species fed infrequently on large numbers of small prey (mean number of prey per stomach = 80.4, range 1–927 items). Remarkably, although they attain almost 1 m in length, the world's largest blindsnakes, *R. schlegelii* and *R. mucruso*, fed on relatively small termites and ant brood. Collectively, our data show that typhlopid snakes have remarkably conservative diets, supporting the idea that the peculiar skull morphology of the Typhlopidae is an adaptation to feeding on small, clumped, immobile prey. Our findings support the hypothesis that the binge-feeding strategy of typhlopid snakes (rapid ingestion of prey, low feeding frequency, and large meal size) evolved to minimize the time spent inside ant nests and, thus, to reduce the risk of prey-inflicted injuries.

Modern snakes (clade Macrostromata) are characterized by their ability to subdue and swallow large prey (Rieppel, 1988). Not surprisingly, dietary demands are believed to have been crucial in the evolutionary origin and radiation of snakes (Gans, 1961; Rieppel, 1980; Greene, 1983; Lee et al., 1999). Evolutionary changes that increased lower jaw mobility allowed the first snakes to ingest larger prey than their lizard ancestors, which in turn facilitated

a fundamental shift in foraging mode from frequent feeding on relatively small prey, to infrequent feeding on relatively large prey (Greene, 1983). Although many recently evolved ophidian clades display the latter “snake-like” foraging mode, members of one basal snake clade—the Scolecophidia (wormlike burrowing snakes from three families)—display a very different feeding strategy: infrequent ingestion of huge numbers of tiny prey (Thomas, 1985; Webb and Shine, 1993a; Webb et al., 2000a).

What factors have favored the evolution of microphagy within the Scolecophidia? Greene

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(1997) suggested that basal scolecophidians have retained the ancestral lizardlike feeding mode (ingestion of numerous tiny prey). This idea is consistent with the phylogenetic position of the Scolecophidia between lizards and all other living snakes (clade Alethinophidia) and supports the widely held belief that snakes evolved from small, burrowing ancestors (Walls, 1940; Bellairs and Underwood, 1951; Rieppel, 1988). However, recent studies have argued that snakes evolved from large marine predators (mosasaurs) with wide gapes (Lee, 1998; Caldwell, 1999; Lee et al., 1999). The marine-ancestor hypothesis remains controversial (see Greene and Cundall, 2000a,b; Lee et al., 2000), but it implies that microphagy—the foraging mode of most scolecophidians—is a highly derived state that appeared later, rather than earlier, in snake evolution (Lee et al., 1999; Scanlon and Lee, 2000).

Scolecophidian prey-transport mechanisms are unique among snakes, consistent with the notion these mechanisms are derived (Iordansky, 1997; Kley and Brainerd, 1999). Unlike most “advanced” snakes that swallow large bulky prey slowly, blindsnakes swallow small prey extremely rapidly (83 prey per minute: Webb and Shine, 1993b). This rapid ingestion of prey is facilitated by the highly derived jaw structures of blindsnakes and specialized prey transport modes. Modern snakes swallow large prey using “pterygoid walk,” in which the snakes’ toothed upper jaws are alternatively ratcheted over the prey, thereby “walking” the snake’s head over and around the prey (Gans, 1961; Cundall, 1987). In contrast, leptotyphlopoid snakes rapidly “rake” small prey into the esophagus by synchronously rotating the toothed lower jaws in and out of the mouth (Kley and Brainerd, 1999). Typhlopoid snakes also rapidly rake prey into the esophagus, but they do this by asynchronously protracting and retracting the highly mobile toothed maxillary bones of the upper jaws (Thomas, 1985; Webb and Shine, 1993b; Iordansky, 1997).

What ecological factors have favored the evolution of these fundamentally different prey transport modes within the Scolecophidia? Recently Kley and Brainerd (1999) suggested that mandibular raking in leptotyphlopoid snakes evolved to minimize the time spent inside ant nests, thereby reducing the risks of prey-inflicted injuries to the predator. However, to evaluate this hypothesis, we need detailed information on the dietary habits of blindsnakes. Although there are > 300 species of living scolecophidians, we know little about their biology, and there are few detailed dietary studies for most species (Greene, 1997). Studies on Australian blindsnakes (*Ramphotyphlops*) and North Amer-

ican and African threadsnakes (*Leptyotyphlops*) revealed that these snakes feed mostly on the larvae and pupae of ants (Punzo, 1974; Webb and Shine, 1993a; Webb et al., 2000a). However, the finding that one tropical typhlopoid (*Acuto-typhlops subocularis*) feeds on earthworms (Webb and Shine, 1993a) highlights the need for dietary studies on additional taxa.

To date, few studies have examined the link between morphology, feeding mode, and diet in scolecophidians (Greene, 1997; Kley and Brainerd, 1999). African blindsnakes are well suited for such an analysis: they display a diversity of body sizes and have highly mobile toothed maxillae that may serve to rake small prey into the esophagus. If prey raking has evolved to maximize prey intake rate (and minimize time spent within ant nests), we might expect the African species to feed on small clumped prey (ant pupae). However, the African blindsnake radiation includes the world’s largest blindsnake (*Rhinotyphlops schlegelii*) that attains lengths of 1 m and body diameters of 5 cm. Plausibly, this large blindsnake could physically ingest larger, and taxonomically more diverse prey, than smaller blindsnakes (e.g., Webb and Shine, 1993a,b). Here we investigate the link between snake size and prey size among five species of blindsnakes from Southern Africa that differ considerably in body shapes and sizes. Although our focus is on feeding ecology, we also provide information on sexual size dimorphism and reproductive biology of these poorly known fossorial snakes.

MATERIALS AND METHODS

We studied five species of blindsnakes from Southern Africa that span a large range of body shapes and sizes and are well represented in museum collections. We studied two slender-bodied blindsnakes, *Typhlops fornasinii* and *Rhinotyphlops lalandei*, and four heavy-bodied taxa, *Typhlops bibronii*, *Rhinotyphlops mucruso*, and two southern races of *Rhinotyphlops schlegelii*. The slender-bodied *T. fornasinii* attains lengths of 18 cm and inhabits alluvial sands in coastal bush and grassland in northeastern South Africa and Mozambique (Fig. 1; Branch, 1998). *Rhinotyphlops lalandei* is a longer (to 35 cm) beak-snouted blindsnake with a wide distribution throughout temperate regions of southern Africa. *Typhlops bibronii* is the smallest of the heavy-bodied blindsnakes (to 48 cm) and is found in highveld and coastal grassland in northern and eastern South Africa (Fig. 1; Branch, 1998).

Schlegel’s blindsnake *R. schlegelii* is the largest blindsnake in the world and is polytypic (Rouxesteve, 1974; Broadley, 1990). Currently three southern subspecies *Rhinotyphlops schlegelii* schle-

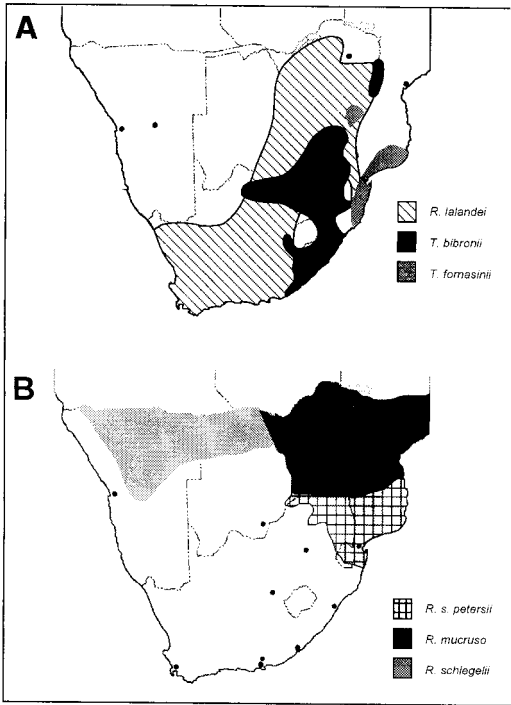


FIG. 1. Distribution of (A) *Rhinotyphlops lalandei*, *Typhlops bibronii*, *Typhlops fornasinii*, and (B) *Rhinotyphlops mucruso*, *Rhinotyphlops schlegelii petersii*, and *Rhinotyphlops schlegelii* in southern Africa (Branch, 1998).

gellii, *R. mucruso* (= *Rhinotyphlops schlegelii dinga*), and *Rhinotyphlops schlegelii petersii* and an isolated northern race *Rhinotyphlops schlegelii brevis* are recognized (Roux-estève, 1974; Broadley, 1990; Branch, 1998). Here we treat *R. mucruso* as a full species and *R. s. petersii* as a western race of *R. schlegelii* (D. Broadley, pers. comm.). *Rhinotyphlops mucruso* has both striped and blotched color morphs and is found in eastern Botswana and the extreme northern parts of South Africa, Zimbabwe, northern Mozambique, and Kenya (Fig. 1; Branch, 1998). *Rhinotyphlops schlegelii petersii* only occurs as a blotched phase and is found in northern Namibia and Botswana to southern Angola, whereas *R. s. schlegelii* occurs as a uniform and blotched phase and is found in northeastern South Africa, southern Mozambique, and eastern Botswana (Fig. 1; Branch, 1998).

We examined all suitable preserved specimens of *T. bibronii* ($N = 253$), *T. fornasinii* ($N = 21$), *R. lalandei* ($N = 226$), *R. mucruso* ($N = 39$), *R. s. petersii* ($N = 46$), and *R. s. schlegelii* ($N = 64$) in the collections of the Transvaal Museum (Pretoria, South Africa), the Port Elizabeth Museum (Eastern Cape, South Africa), the State Museum of Namibia and the Directorate of Wildlife Conservation (both in Windhoek, Na-

mibia). For each specimen, we measured snout-vent length (SVL) and tail length with a ruler (to the nearest millimeter). For specimens in good condition, or those containing prey in stomachs, we measured head width (HW) level with the eyes, mouth width (MW) at the rear-most part of mouth, and midbody diameter (MBD) with vernier calipers (to the nearest 0.1 mm). Each specimen was carefully opened with a midventral incision so we could examine the gonads and alimentary tract. Our criteria for sexual maturity were as follows: males, enlarged turgid testes or opaque, thickened efferent ducts; females, thickened muscular oviducts, vitellogenic ovarian follicles, or oviductal eggs. Prey items were removed from the alimentary tract and placed in vials for later identification. We identified prey to the ordinal level (where possible) and recorded the total number of each larval stage of prey item (i.e., adults, eggs, larvae, pupae). Because blindsnakes ingested prey items whole, with no mastication, we were unlikely to count the same prey item in different parts of the gut. However, although we found intact pupal cases and larval exoskeletons in blindsnake recta, usually only the heads of adult insects remained intact. Thus, our counts of adult stages were based on whole insects or heads but not pieces of soft body parts. We measured the length and maximum diameter of the largest and smallest prey item and the lengths and diameters of five specimens of the most frequently ingested prey type (with vernier calipers, to nearest 0.1 mm).

We used analysis of covariance to investigate whether there was divergence between the sexes in morphological traits (tail length, head width, mouth width, and midbody diameter) relative to SVL. We used sex as the factor, SVL as the covariate, and TL, HW, MW, and MBD as the dependent variables in one-factor ANCOVAs for each of five species (we excluded *T. fornasinii* because sample sizes were too small).

RESULTS

Morphology and Sexual Size Dimorphism.—Body sizes (SVL, TL, mass) and morphological traits (HW, MW, MBD) of African blindsnakes are shown in Table 1. Significant sexual size dimorphism was evident in all species except the smallest species, *T. fornasinii* (Table 1). In the sexually dimorphic species, adult females had significantly larger mean SVLs, attained larger body sizes, had wider heads and mouths, matured at larger sizes, and were more heavy-bodied (had larger midbody diameters) than conspecific males (t -tests for these traits, $P < 0.01$ for each species). Adult females were significantly heavier (blotted-dry mass) than males in *T. bibronii*, *R. mucruso*, and both races of *R. schle-*

gellii (*t*-tests, $P < 0.01$). Females of the three latter taxa also had longer tails than males (*t*-tests, $P < 0.01$).

ANCOVA revealed that males had significantly longer tails than did females with similar body lengths in *T. bibronii*, *T. lalandei*, *R. mucruso*, and *R. s. petersii* (slopes tests: *F*-values = 0.80–3.38, NS; sex: *F*-values = 4.16–39.43, $P < 0.05$) but not *R. s. schlegelii* (slopes $F_{1,44} = 1.71$, $P = 0.20$, sex $F_{1,45} = 1.37$, $P = 0.25$). In *T. lalandei*, there were significant sex-differences in head width (slopes $F_{1,92} = 0.01$, $P = 0.92$, sex $F_{1,93} = 4.23$, $P = 0.04$), mouth width (slopes $F_{1,92} = 0.04$, $P = 0.85$, sex $F_{1,93} = 4.85$, $P = 0.03$), and mid-body diameter (slopes $F_{1,92} = 0.30$, $P = 0.58$, sex $F_{1,93} = 4.01$, $P = 0.05$) relative to SVL. That is, female *T. lalandei* had wider heads and mouths and were more heavy-bodied than males of the same body length. In the remaining four taxa, we found no sexual differences in morphological traits relative to SVL. Thus, with the exception of tail length, sexual size dimorphism in three of four taxa (with the exception of *T. lalandei*) was a result of the larger overall size (SVL) of adult females compared to males, rather than any sexual divergence in the relative size of bodily structures.

Reproductive Biology.—There were no reproductive females of *T. fornasinii* in the museum collections that we examined. For the remaining species, gravid females contained shelled eggs, indicating oviparity. Mean clutch sizes varied among species: *T. bibronii* mean = 6.6, range 2–13, $N = 21$; *R. lalandei* 4.0, 2–8, $N = 15$; *R. mucruso* = 9.3, 8–11, $N = 3$; *R. s. petersii* = 25.0, 18–32, $N = 2$; *R. s. schlegelii* = 7.0, $N = 1$. We found significant positive correlations between maternal body size (SVL) and clutch size (numbers of oviductal eggs) in *T. bibronii* ($r = 0.50$, $N = 20$, $P = 0.03$) and *R. lalandei* ($r = 0.66$, $N = 15$, $P < 0.01$). Examination of ovarian follicles in preserved specimens showed that the temperate zone *T. bibronii* and *R. lalandei* had highly seasonal reproductive cycles, with vitellogenesis in spring (September to November) and oviposition in summer (December to February, Fig. 2). Male *T. bibronii* and *R. lalandei* collected in July, August, September, and October had large turgid testes (with sperm in efferent ducts), which suggests that mating occurs in winter or spring. In contrast, reproductive males of *R. mucruso*, *R. s. petersii*, and *R. schlegelii* were found in the months of December, February, March, April, and May. There were too few reproductive females with dates of collection to infer female reproductive cycles for these species. However, one gravid female *R. s. petersii* (TM 49908) was collected in late May, whereas a gravid *R. schlegelii* (TM 30015) was collected in February.

Prey Types.—Examination of 7151 prey items

from the alimentary tracts (stomachs, small intestines, rectums) of 112 individuals revealed that African blindsnakes fed mainly on the larvae and pupae of ants and termites (Table 2). All prey items (including adult stages) found in stomachs were ingested whole, with little evidence of physical damage during ingestion. Adult ants were rarely ingested by blindsnakes ($< 7.0\%$ of the diets), but adult termites were consumed by *R. mucruso* (18.4% of prey items, 14.3% of stomachs) and *T. bibronii* (21.4% of stomachs, see Table 2). A high proportion of blindsnakes (93%) had consumed only one prey type (ants or termites, but not both), suggesting that they had fed within a single nest. Seven blindsnakes had consumed ants and termites, whereas one *R. lalandei* had ingested 18 insect pupae along with nine adult ants and 136 ant pupae. One adult female *T. bibronii* (SVL = 260 mm) had eaten a small adult beetle, four adult ants, 180 ant larvae, five ant pupae, and eight adult termites.

Meal Sizes.—Eighty-five of 649 typhlopoid snakes (13.1%) contained prey in stomachs. The proportion of snakes with food in stomachs ranged from 8.7% in *R. s. petersii* to 23.8% in *T. fornasinii* (Table 3). Blindsnakes of all body sizes consumed large numbers of prey in a single meal, and numerous blindsnakes contained prey in their entire digestive tracts, including their mouths and esophagi. Larger snakes did not ingest more prey than their smaller conspecifics (intraspecific correlations between SVL and total number of prey, all NS). The maximum number of prey items recorded in typhlopoid stomachs ranged from 38 in *R. s. petersii* to 927 in *R. lalandei* (Table 3). The mean number of prey in stomachs also varied interspecifically and ranged from 15.8 in *R. s. petersii* to 133.0 in *T. fornasinii* (Table 3). An interspecific comparison revealed a significant negative correlation between blindsnake body size (mean SVL) versus mean meal size ($r = -0.86$, $P = 0.03$); that is, larger species of blindsnake contained fewer prey in stomachs than did smaller species.

Seasonality of Feeding.—Seasonal patterns of feeding were evident in two species from temperate zones, *T. bibronii* and *R. lalandei* (Fig. 3). Both species fed mainly during spring and summer, and significantly fewer *T. bibronii* contained prey in stomachs during autumn and winter compared to spring and summer ($\chi^2 = 14.39$, 3 df, $P = 0.002$). In both species, the proportions of snakes containing prey in stomachs during summer were low (21.4% for *T. bibronii*, 20.5% for *R. lalandei*, Fig. 3).

Predator-Prey Size Relationships.—Unlike advanced snakes, typhlopoid snakes do not have a free intramandibular hinge and have only limited lower jaw mobility (lordansky, 1997). This

TABLE 1. Morphology of adult *Typhlops* and *Rhinotyphlops* from Southern Africa. Table shows mean values and ranges with SD in parentheses. Linear measurements are in millimetres; all measurements (including mass) were taken from preserved museum specimens. Sample sizes for each sex are shown in parentheses.

Morphology	<i>T. bibronii</i>		<i>T. fornasinii</i>		<i>R. lalandei</i>	
	Males (93)	Females (85)	Males (7)	Females (8)	Males (59)	Females (102)
Snout-vent length	253.5 (31.7)	319.9 (60.1)	137.0 (20.0)	143.8 (15.9)	205.7 (38.5)	242.2 (41.3)
SVL range	198–340	230–477	110–175	123–160	146–315	171–340
Tail length	5.1 (1.0)	5.4 (1.2)	3.3 (0.5)	2.9 (0.6)	4.3 (0.8)	4.1 (0.9)
TL range	3–8	3–9	3–4	2–4	3–6	2–6
Head width	5.1 (0.6)	6.0 (1.0)	2.9 (0.3)	3.1 (0.3)	3.7 (0.6)	4.4 (0.8)
HW range	4.0–6.6	4.6–8.4	2.5–3.4	2.7–3.5	2.5–5.5	3.1–5.9
Mouth width	3.4 (0.4)	3.9 (0.7)	1.9 (0.2)	2.1 (0.3)	2.3 (0.5)	2.9 (0.6)
MW range	2.5–4.4	3.0–5.4	1.6–2.2	1.7–2.5	1.5–3.5	1.8–4.3
Midbody diameter	7.6 (1.4)	9.3 (2.6)	4.4 (0.7)	4.9 (0.8)	5.2 (1.1)	6.4 (1.2)
MBD range	5.0–11.7	5.7–16.7	3.8–6.0	3.9–6.3	3.3–9.0	4.0–9.1
Mass (g)	13.8 (6.6)	34.7 (19.1)	—	—	—	—
Mass range	6–24	9–75	—	—	—	—

cranial morphology may restrict the ability of African typhlopids to swallow large prey. To investigate this possibility, we examined relationships between predator gape (mouth width) and prey size (length and diameter) in *R. lalandei* and *T. bibronii*, the species with large sample sizes. In both species, snakes with wider mouths ate larger prey (correlations between blindsnake mouth width and: maximum prey length, *T. bibronii* $r = 0.40$, $N = 29$, $P = 0.03$; *R. lalandei* $r = 0.74$, $N = 17$, $P = 0.0008$; maximum prey diameter, *T. bibronii* $r = 0.41$, $N = 31$, $P = 0.02$; *R. lalandei* $r = 0.56$, $N = 21$, $P = 0.008$). Although larger individuals ate wider prey than smaller conspecifics, few blindsnakes had ingested prey items that were larger than their mouth width (Fig. 4).

DISCUSSION

The results of this study agree with anecdotal accounts of previous authors but provide additional information on reproduction and feeding biology of African blindsnakes. Previous accounts have correctly stated that female *Typhlops* are oviparous with large clutch sizes (e.g., FitzSimons, 1962; Branch, 1998). Although it is oviparous, *T. bibronii* lays eggs at an advanced stage of development, which hatch within a few days of laying (Erasmus and Branch, 1983). Egg laying has been recorded in January (one clutch, Yeadon, 1991), February (three clutches, Erasmus and Branch, 1983), and March (three clutches, Jacobsen, 1989). The seasonal timing of reproduction of *T. bibronii* and *R. lalandei* (vitellogenesis in spring, oviposition in summer, hatching in autumn) is consistent with that of typhlopoid snakes from cool temperate climates (Shine and Webb, 1990) and most snakes of

southern Africa (Branch, 1998). However, we still have little information on the timing of reproduction in the larger tropical blindsnakes. Our small dataset for *R. schlegelii*, *R. s. petersii*, and *R. mucruso* from southern Africa suggests that mating occurs in summer and early autumn, with females laying eggs in late summer and midyear. Thus, in contrast to temperate-zone blindsnakes, the timing of reproduction in blindsnakes from tropical regions may be highly variable, similar to other squamates (James and Shine, 1985). For example, in some species from the wet-dry tropics of northern Australia, reproduction coincides with rainfall, whereas in other species reproduction occurs year-round (James and Shine, 1985). Future studies on the timing of reproduction in African blindsnakes from tropical regions would be of great interest.

Sexual dimorphism in mean adult body size has been noted previously in *T. bibronii* (Branch, 1997) and is considerable in the African blindsnakes we studied. Using the index proposed by Gibbons and Lovich (1990), African typhlopids have dimorphism indices ranging from 1.1–2.0. This is higher than seen in most other snakes but similar to that reported for other scolecophidians (Shine and Webb, 1990; Shine, 1993). Our data on African typhlopids also reveal a phenomenon seen in other snakes, including other scolecophidians: the degree of sexual size dimorphism varies with absolute body size (Shine, 1993). Within the African typhlopids, the degree to which females exceed males in mean adult size increases in the larger species (regression of SSD index against mean adult SVL: $r = 0.93$, $N = 6$, $P = 0.007$). Typhlopids also resemble "higher" snakes in the tendency for males to have relatively longer tails

TABLE 1. Extended.

<i>R. mucruso</i>		<i>R. s. petersii</i>		<i>R. s. schlegelii</i>	
Males (13)	Females (11)	Males (15)	Females (19)	Males (18)	Females (20)
257.3 (29.0)	439.1 (83.8)	257.3 (29.4)	435.1 (126.6)	256.7 (43.7)	518.2 (139.0)
200–300	320–630	215–315	280–655	183–320	305–820
4.3 (0.9)	6.2 (1.6)	4.9 (1.0)	6.1 (1.4)	5.0 (1.1)	7.7 (2.3)
3–6	5–10	4–7	4–8	3–7	4–12
6.9 (0.9)	9.5 (1.7)	6.7 (0.5)	9.2 (1.8)	6.8 (0.9)	10.5 (1.8)
5.0–8.1	7.1–13.2	6.0–7.5	5.5–11.9	5.1–8.5	6.6–13.5
4.3 (0.7)	5.9 (1.0)	4.0 (0.4)	5.6 (1.2)	4.3 (0.6)	6.7 (1.3)
3.1–5.8	4.7–8.2	3.2–4.5	3.2–7.4	2.9–5.2	4.2–8.7
10.2 (2.3)	13.7 (3.9)	9.5 (1.1)	15.8 (6.0)	9.5 (1.8)	18.1 (6.4)
6.9–15.5	8.6–19.8	8.0–11.7	6.5–26.4	5.7–12.1	8.6–28.8
19.6 (8.9)	63.6 (50.2)	16.9 (6.3)	101.3 (93.6)	16.6 (8.6)	134.6 (123.9)
8–40	20–180	10–27	8–280	6–30	10–380

than conspecific females. Males have longer tails relative to SVL in a diverse array of snake taxa, possibly reflecting the need for males to fit their hemipenes inside the tailbase (e.g., King, 1989; Shine, 1993).

Most previous reports have stated that African blindsnakes feed on "ants and termites" (e.g., Branch, 1998). Our data show that African blindsnakes feed mainly on the larvae and pupae of ants, rather than on the adult stages. This preference for the immature stages of ants mirrors the situation seen in African leptotyphlopids (Webb et al., 2000a) and Australian typhlopids (Webb and Shine, 1993a). Adult ants contain much indigestible chitin and are much less nutritious than the soft larval stages. Unlike adult ants, termites are soft-bodied, and

represent a major prey resource for many fossorial reptiles in southern Africa (e.g., Branch, 1998; Webb et al., 2000a). Five of six blindsnake species ate adult termites, but only a relatively small proportion of snakes (10–22%) contained this prey type. Similarly, termites accounted for a low proportion (1.9–7.2%) of the numerical diets of all species except *R. mucruso* (38.4%, Table 3). This mirrors the situation in Australia, where only one tropical species *Ramphotyphlops polygrammicus* feeds on termites to a significant degree (9% of total diet, Webb and Shine, 1993a).

The low reliance on termites as a food source by African typhlopids is puzzling, especially considering the high diversity and abundance of termites in southern Africa (Coaton and Sheasby, 1972). The low degree of termitophagy by African blindsnakes could be related to the insects' well-developed defense mechanisms. For example, soldiers of African *Trinervitermes* possess highly effective chemical defense secretions that prevent most myrmecophagous mammals from specialising on them (Richardson and Levitan, 1994). Chemical sprays from soldiers could deter blindsnakes from entering termite nests or could block or anaesthetize the snakes' sensory organs on the facial region, thereby preventing them from feeding (Thomas, 1985). Soldiers of African *Macrotermes* use their sharp mandibles for mechanical defense and possess a sophisticated system of long-distance alarm communication. When disturbed in gallery systems, soldiers drum their heads against the substratum, resulting in a retreat of termites to the nest (Rohrig et al., 1999). Whether blindsnakes trigger these sophisticated termite defense systems is not known, but could be tested in the field

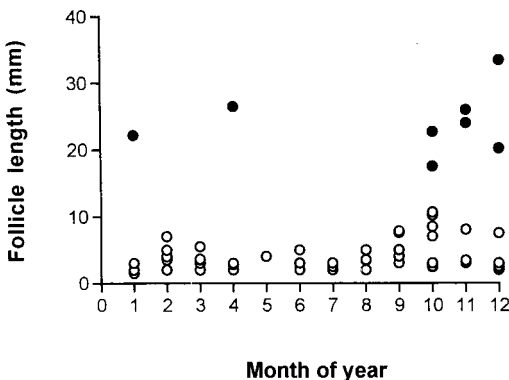


FIG. 2. Seasonal variation in the lengths of the largest ovarian follicles (open circles) and oviductal eggs (solid circles) in adult female *Typhlops bibronii* from southern Africa.

TABLE 2. Prey items found in the alimentary tracts of *Typhlops* and *Rhinotyphlops* from southern Africa. N = number of prey items, % = percentage of the total number of prey items, and F = frequency of occurrence of each type of prey item. Sample sizes for each species are shown in parentheses.

Prey taxon	Larval stage	T. hibronii (42)			T. forusisnii (5)			R. lalandei (29)			R. mucroso (14)			R. s. petersii (8)			R. s. schleggelli (14)		
		N	%	F	N	%	F	N	%	F	N	%	F	N	%	F	N	%	F
Acarina	adults	14	0.6	2.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Coleoptera	adults	1	0.0	2.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hymenoptera	adults	114	4.6	38.1	21	3.2	60.0	62	2.4	41.4	14.3	6	4.4	25.0	1	0.3	7.1	—	—
	eggs	—	—	—	—	—	—	255	9.8	6.9	—	—	—	—	—	—	—	—	—
	larvae	407	16.3	28.6	80	12.0	80.0	538	20.7	37.9	28.6	14	10.2	25.0	8	2.3	7.1	—	—
	pupae	1782	71.3	66.7	564	84.8	100.0	1684	64.7	86.2	78.6	106	77.4	62.5	324	93.6	92.9	—	—
Isopoda	adults	175	7.0	21.4	—	—	—	47	1.8	6.9	14.3	11	8.0	25.0	13	3.8	14.3	—	—
	immatures	8	0.3	2.4	—	—	—	—	—	—	7.1	—	—	—	—	—	—	—	—
	pupae	—	—	—	—	—	—	18	—	—	7.1	—	—	—	—	—	—	—	—
Unidentified	Totals	2501	—	—	665	—	—	2604	—	—	898	—	—	137	—	—	—	—	346

(see Rohrig et al., 1999). Alternatively, interspecific dietary differences among African blindsnakes could simply reflect differences in burrowing ability or in the "adaptive zones" (soil types and depths) inhabited by particular species. The species most reliant on termites, *R. mucroso* has a beaked snout and is thought to live deep underground (Branch, 1998). Short-term field telemetry studies on this large heavy-bodied species would be feasible and would greatly enhance our overall understanding of this much-neglected group of snakes.

Few African *Typhlops* and *Rhinotyphlops* contained prey in stomachs, which suggests that these snakes feed infrequently. Low rates of feeding are found in other scolecophidians including African *Leptotyphlops* (Webb et al., 2000a) and Australian *Ramphotyphlops* (Webb and Shine, 1993a). Our findings are the result of any bias in the collection or preservation of specimens, because many snakes were found dead by museum staff in the eastern water carrier in Namibia (Griffin et al., 1989). Significantly, a higher proportion of amphisbaenians (*Monopeltis anchietae* and *Zygaspis quadrifrons*) from the same museum collections contained prey in stomachs than did sympatric blindsnakes (147 of 216 amphisbaenians versus 84 of 649 blindsnakes, $\chi^2 = 123.05$, $P < 0.0001$, Webb et al., 2000b).

Why do the African typhlopoid snakes that we studied feed infrequently? Low rates of feeding by Australian *Ramphotyphlops* have been attributed to their reliance on a food supply that is spatially or temporally variable (Webb and Shine, 1993a). However, it is equally plausible that the "binge feeding strategy" of typhlopoid snakes, whereby large numbers of prey are taken from a single ant nest, may be an adaptation to feeding inside the nests of potentially dangerous prey (Kley and Brainerd, 1999). Most ants bite, sting, or spray chemical secretions on intruders and defend nests vigorously (e.g., Blum, 1981; Webb and Shine, 1993b). The risks of ant-inflicted injuries may be minimized by blindsnakes entering nests infrequently and taking large meals each time. The general occurrence of this binge-feeding strategy (low feeding frequency coupled with large meal size) in five taxa of fossorial worm-like reptiles that forage inside ant nests (pygopodid lizards of the genus *Aprasia*—Webb and Shine, 1994; and four genera of blindsnakes: *Ramphotyphlops*—Webb and Shine, 1993a; *Leptotyphlops*—Webb et al., 2000a; *Rhinotyphlops*, *Typhlops*—this study) supports the predator-vulnerability hypothesis. Infrequent feeding may provide additional benefits to blindsnakes. For example, active searching for prey may be energetically costly or may expose

TABLE 3. Frequency of feeding by African *Typhlops* and *Rhinotyphlops*. The table shows the mean number of prey items found in stomachs, with standard deviations in parentheses.

Blindsnake species	Number examined	Number with prey in stomach	Percent with prey in stomach	Mean number of prey items per stomach (SD)	Range
<i>T. bibronii</i>	253	31	12.3	75.9 (103.3)	2-490
<i>T. fornasinii</i>	21	5	23.8	133.0 (181.2)	43-457
<i>R. lalandei</i>	226	27	11.98	95.9 (182.1)	1-927
<i>R. mucruso</i>	39	9	23.1	92.8 (121.0)	15-307
<i>R. s. petersii</i>	46	3	6.5	25.7 (11.2)	16-38
<i>R. s. schlegelii</i>	64	10	15.6	31.4 (19.6)	1-67

blindsnakes to predators, especially if the snakes follow above-ground ant trails (Gehlbach et al., 1971; Webb and Shine, 1992). Infrequent feeding could thereby reduce the snakes' exposure to avian or snake predators and would enable energetic savings through down-regulation of the gut during long periods between meals (e.g., Secor and Diamond, 1995).

How do African blindsnakes avoid the stings of potentially dangerous prey? At least one species of North American blindsnake (*Leptotyphlops dulcis*) uses cloacal secretions to repel ant attacks (Gehlbach et al., 1968; Watkins et al., 1969), but we do not know whether this behavior is utilized by African *Rhinotyphlops* and *Typhlops*. The African blindsnakes we studied fed on ants that were small relative to snake size (Fig. 4) so that the snakes' highly polished body scales may provide adequate protection from ant attacks (Webb and Shine, 1993b). Simple laboratory experiments to test these alternative hypotheses (body size vs. cloacal secretions) would be of great interest.

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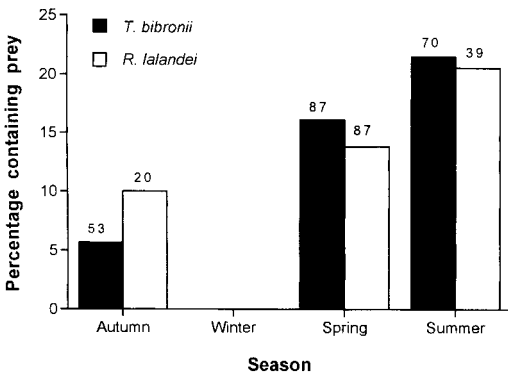


FIG. 3. Seasonal variation in the proportions of *Typhlops bibronii* and *Rhinotyphlops lalandei* containing prey in stomachs. Numbers above histograms refer to the total number of snakes collected during that season. Although 43 *T. bibronii* and 29 *R. lalandei* were collected during winters, none of these snakes contained food in stomachs.

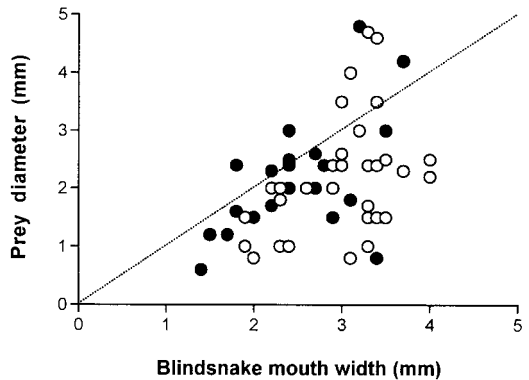


FIG. 4. The relationship between blindsnake mouth width and the diameter of the largest prey item ingested in stomachs of *Typhlops bibronii* (open circles) and *Rhinotyphlops lalandei* (solid circles). The dotted line shows where prey diameter = mouth width (as measured on preserved museum specimens). Unlike advanced snakes, African blindsnakes do not ingest prey that is large relative to snake head size.

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