

Original article

Feeding ecology, reproduction and sexual dimorphism in the colubrid snake *Crotaphopeltis hotamboeia* in southern Africa

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Abstract.—We examined museum specimens to quantify diet, reproductive cycles and sexual dimorphism in body size of the colubrid snake *Crotaphopeltis hotamboeia*. Females attain sexual maturity at approximately 300 mm snout-vent length (SVL) and males at approximately 240 mm SVL. Females grow larger than males (maximum SVLs of 830 vs 700 mm SVL), and also have longer and wider heads and wider bodies than do males of the same body length. Males have relatively longer tails than females, but eye size relative to head length shows no sexual dimorphism. Both sexes breed each year. Females commence vitellogenesis in late winter (September) and oviposit from October to January. Clutch size ranged from four to 12 eggs with a mean of 7.58 and was highly correlated with female SVL. The testes of adult males are turgid throughout the year, suggesting a prolonged mating season. Of 73 prey items recorded, 97% were anurans. Six anuran families were represented among the prey items, but bufonids (39%), ranids (29%) and microhylids (25%) comprised most of the 51 anuran food items identified to genus. Larger snakes ate larger prey items, in terms of SVL as well as mass. However, the snake's sex and age (adult vs juvenile) did not affect prey type. Bufonids, microhylids and ranids were consumed by snakes of all ages and both sexes, and were eaten all year except during mid-winter (July and August).

Key words.— Dietary habits, allometry, ecology, colubrid.

The endemic African colubrid snake genus *Crotaphopeltis* comprises six species that range from West Africa to the Cape Province of South Africa (Branch 1998). *Crotaphopeltis* species are all small to medium-sized snakes, usually associated with mesic habitats, including lowland swamps and marshes (*C. hotamboeia*), flood plains (*C. barotseensis*, *C. degeni*, and *C. braestrupi*; Broadley 1968; Rasmussen 1985, 1997), or montane rain forest (*C. tornieri*; Rasmussen 1993). Roman (1974) described *C. acarina* from Burkina Fasso, but this was subsequently synonymised with *C. hippocrepis* (Rasmussen 1993); its preferred habitat remains unknown.

Although there is much anecdotal information on diet, clutch size and sexual dimorphism in scale counts of the species within this genus

(e.g. Pitman 1974; Broadley 1983; Rasmussen 1985, 1993, 1997), there is little quantitative data, especially on topics such as male reproductive cycles or sexual size dimorphism. To obtain more detailed information, we chose to study southern populations of the Red-lipped or Herald snake, *Crotaphopeltis hotamboeia*, which is one of the most common snakes in mesic habitats in the eastern regions of southern Africa. Within the genus it is also the only member represented in large numbers in museum collections. Based on the dissection of museum specimens and a review of the literature, we present detailed data on male and female reproductive cycles, juvenile and adult diet and sexual size dimorphism for southern populations of *C. hotamboeia*, and make comparisons, where possible, with other *Crotaphopeltis* species.

MATERIALS AND METHODS

A total of 398 museum specimens were examined from the Port Elizabeth Museum, the Transvaal Museum (Pretoria) and the National Museum (Bloemfontein) in South Africa. Only specimens from southern Africa were examined to control for major geographic variation in reproductive patterns. A mid-ventral incision was made to allow us to examine the alimentary canal for food items and score reproductive condition. Small incisions were made in the stomach and the hindgut and any identifiable prey items were removed for identification. Sex was determined by either direct examination of the gonads or by making a small incision in the base of the tail to check for hemipenes in eviscerated specimens. Males were recorded as sexually mature if testes were thick (as opposed to flat and ribbon like in immature males), and sexually active at the time of preservation if testes were turgid and/or the efferent ducts were opaque due to the presence of sperm. Females were recorded as sexually mature if the oviducts appeared muscular, and sexually active at the time of preservation if large ovarian follicles or eggs were present. The diameter of the largest follicle or egg was recorded, as was the number of follicles or eggs if larger than 8 mm. For 158 of these specimens we also recorded the following morphological variables to examine sexual size dimorphism: snout-vent length (SVL), head length, head width at the widest point, eye diameter, and mid-body width. Body size variables were log transformed prior to analyses to meet the assumptions of the statistical tests we employed. We used unpaired two-tailed t-tests and analysis of covariance (ANCOVA) to test for sexual size dimorphism and regression analysis to examine correlations between maternal body size vs clutch size, snake SVL vs prey SVL, and snake mass vs prey mass.

RESULTS

MORPHOLOGY

The largest male and female we recorded were 700 and 830 mm SVL respectively. The small-

est specimen measured had a SVL of 120 mm. Mean values for adult SVL, head length, head width, body width and eye diameter all showed sexual size dimorphism, with females larger in all cases (Table 1). Only tail length did not show dimorphism based on mean sizes (Table 1). However, ANCOVA analyses revealed that the sexes differed in shape as well as absolute body size. Males had longer tails than females of the same body length (Fig. 1a: slopes homo-

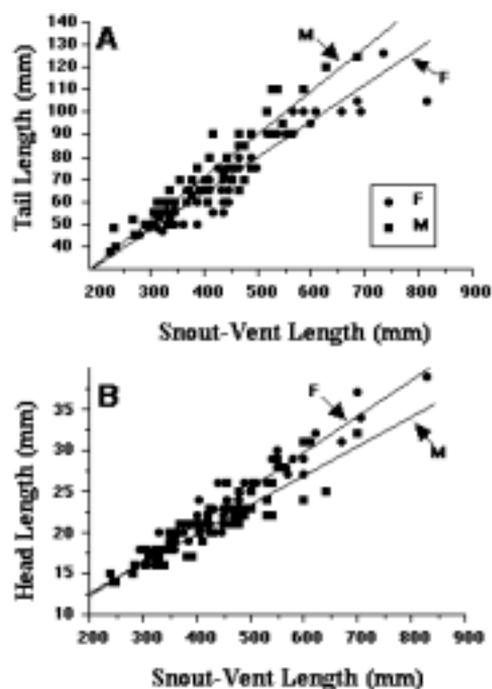


Figure 1. Sexual dimorphism in body proportions in *Crotaphopeltis hotamboeia*, based on measurement of preserved specimens. At the same snout-vent length, males have longer tails than females (A) but shorter heads (B). See text for statistical treatment of these data.

geneous $F_{1,147} = 0.95$, $P = 0.389$; intercepts $F_{1,149} = 21.99$, $P < 0.0001$). Females had longer heads (Fig. 1b: slopes homogeneous $F_{1,147} = 1.83$, $P = 0.1644$; intercepts $F_{1,149} = 16.48$, $P < 0.0001$) and wider heads (slopes homogeneous $F_{1,141} = 0.76$, $P = 0.4707$; intercepts $F_{1,149} = 3.99$, $P < 0.0206$) than males of the same body length. Females also were wider-bodied than

Table 1. Summary of sexual dimorphism morphological traits in *Crotaphopeltis hotamboeia* from southern Africa. The last three columns show results from unpaired two-tailed *t*-tests for sexual size dimorphism. Statistical tests were performed on log transformed data. Measures are in mm.

| Trait | Adult Male | | | Adult Female | | | d.f. | <i>t</i> | <i>P</i> |
|-------------------|------------|---------------|-----------|--------------|---------------|-----------|------|----------|----------|
| | N | Mean ± SD | Range | N | Mean ± SD | Range | | | |
| Snout-vent length | 52 | 420.6 ± 106.4 | 240 - 700 | 73 | 460.6 ± 114.3 | 295 - 830 | 123 | 2.12 | 0.0359 |
| Tail length | 51 | 72.2 ± 21.5 | 38 - 125 | 60 | 72.1 ± 20.2 | 45 - 130 | 109 | 0.06 | 0.9552 |
| Head length | 51 | 20.76 ± 4.23 | 14 - 32 | 59 | 23.66 ± 5.24 | 16 - 39 | 108 | 3.23 | 0.0016 |
| Head width | 48 | 11.48 ± 2.48 | 7 - 18 | 56 | 12.95 ± 3.72 | 8 - 26 | 102 | 2.22 | 0.0284 |
| Body width | 51 | 10.75 ± 1.89 | 7 - 15 | 60 | 12.18 ± 3.25 | 7 - 22 | 109 | 2.49 | 0.0144 |
| Eye diameter | 50 | 3.01 ± 0.48 | 2.0 - 4.0 | 57 | 3.33 ± 0.56 | 2.5 - 4.5 | 105 | 3.14 | 0.0022 |

males of the same body length (slopes homogeneous $F_{1,147} = 0.20$, $P = 0.8180$; intercepts $F_{1,149} = 7.60$, $P < 0.0007$) or head length (slopes homogeneous $F_{1,145} = 1.43$, $P = 0.2435$; intercepts $F_{1,149} = 11.81$, $P < 0.0001$). However, eye size relative to head length did not differ between the sexes (homogeneity of slopes $F_{1,144} = 0.44$, $P = 0.6474$, intercepts $F_{1,146} = 0.50$, $P = 0.6062$).

REPRODUCTION

The smallest female with thickened muscular oviducts, indicating sexual maturity, was 295 mm SVL. All females larger than this size appeared to be in some stage of reproduction, indicating that females reproduce every year once they reach sexual maturity. Clutch sizes determined for 19 clutches ranged from four to 12 eggs (7.58 ± 2.50), and fecundity was significantly correlated with maternal SVL ($R = 0.53$, $N = 19$, $P < .0205$; Fig. 2a). A plot of ovarian follicle or egg diameter against the month of capture reveals that ovarian follicles were less than 10 mm throughout late summer, autumn and winter (Feb. - Aug.) and vitellogenic in late winter through to spring and early summer (Sept. - Jan.; Fig. 2b). Females appear to yolk their ovarian follicles rapidly, starting in September. Egg deposition commences in October and continues through January.

The smallest male with thickened efferent ducts and at least semi-turgid testes, indicating sexual maturity, was 240 mm SVL. Virtually all males larger than this size displayed at least semi-turgid testes (Fig. 3a). In most adult males

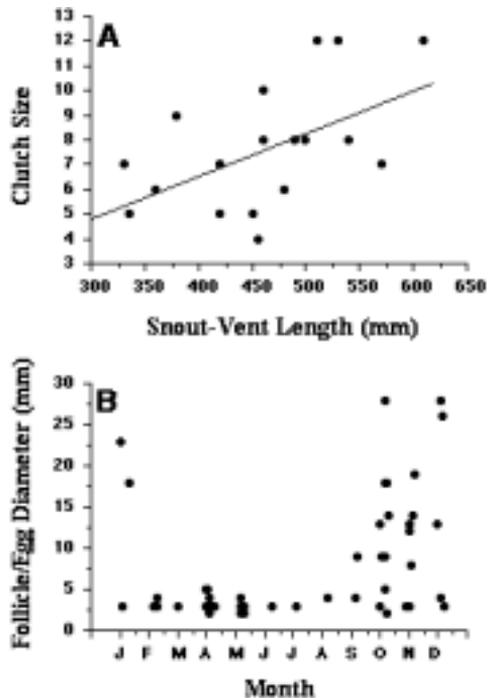


Figure 2. Reproductive biology of female *Crotaphopeltis hotamboeia*. The upper graph (A) shows that larger females produce larger clutches of eggs, whereas the lower graph (B) shows that the ovarian follicles and oviductal eggs are largest during spring and summer.

testes were turgid for much of the year, with visibly opaque efferent ducts (indicating the presence of sperm) in many cases. The only significant decrease in testicular activity was in mid-winter (July; Fig. 3b). Thus, spermatogenesis coincides with female follicular development and ovulation, but males appear to main-

Table 2. Prey items identified from the alimentary canals of *Crotrophopeltis hotamboeia* in this study and a summary of prey items identified in the literature.

| Prey Type | Number from this study | Number from literature source | Literature Source |
|-----------------------------------|------------------------|-------------------------------|---|
| Amphibia | | | |
| Arthroleptidae | | | |
| <i>Arthroleptis stenodactylus</i> | 1 | 1 | FitzSimons 1939 |
| | | 4 | Loveridge 1942 |
| | | 1 | Broadley 1966 |
| <i>Arthroleptis xenodactylus</i> | | 4 | Loveridge 1933 |
| Bufonidae | | | |
| <i>Bufo angusticeps</i> | 1 | | |
| <i>Bufo fenoulheti</i> | 2 | | |
| <i>Bufo gariepensis</i> | 2 | | |
| <i>Bufo garmani</i> | | 1 | Jacobsen 1982 |
| <i>Bufo gutturalis</i> | | 1 | Loveridge 1933 |
| | | 1 | Broadley 1966 |
| <i>Bufo pusillus</i> | | 1 | Broadley 1966 |
| <i>Bufo rangeri</i> | 7 | | |
| <i>Bufo regularis</i> | | 1 | Mertens 1938 |
| | | 1 | Loveridge 1942 |
| <i>Bufo steindachneri</i> | | 1 | Loveridge 1936 |
| <i>Bufo</i> sp. | 6 | several | Loveridge 1936; Hoevers & Johnson 1982 |
| <i>Schismaderma carens</i> | 2 | 2 | Loveridge 1953; |
| | | 1 | Broadley 1966 |
| Ranidae | | | |
| <i>Afrana angolensis</i> | 1 | 1 | Loveridge 1953 |
| <i>Afrana fuscucula</i> | 1 | | |
| <i>Cacosternum boetgeri</i> | 6 | 1 | De Waal 1978 |
| <i>Phrynobatrachus</i> sp. | 1 | | |
| <i>Ptychadena mascareniensis</i> | | 1 | Loveridge 1936 |
| <i>Ptychadena</i> sp. | | 1 | Hoevers & Johnson 1982 |
| <i>Strongylopus grayii</i> | 1 | | |
| <i>Tomopterna cryptotis</i> | 2 | 1 | Broadley 1966 |
| | | 1 | De Waal 1978 |
| Unidentifiable ranid | 2 | 1 | Broadley 1966 |
| Microhylidae | | | |
| <i>Breviceps adspersus</i> | 2 | 1 | Loveridge 1953 |
| <i>Breviceps mossambica</i> | 1 | 1 | Broadley 1966 |
| <i>Breviceps fuscus</i> | 2 | | |
| <i>Breviceps poweri</i> | | 1 | Broadley 1966 |
| <i>Breviceps</i> sp. | 8 | | |
| Hyperolidae | | | |
| <i>Hyperolius argentovittis</i> | | 1 | Loveridge 1942 |
| <i>Kassina senegalensis</i> | 1 | 3 | Jacobsen 1982 |
| Hemisotidae | | | |
| <i>Hemisis marmoratus</i> | 2 | | |
| Unidentifiable amphibian | 20 | several | Schmidt 1923; Barbour & Loveridge 1928; Loveridge 1936; Pakenham 1983 |

Table 2. (continued)

| Prey Type | Number from this study | Number from literature source | Literature Source |
|-------------------------------------|------------------------|-------------------------------|-----------------------|
| Reptilia | | | |
| Gekkonidae | | | |
| <i>Hemidactylus mabouia</i> | | 1 | Loveridge 1942 |
| <i>Pachydactylus capensis</i> | | 1 | De Waal 1978 |
| <i>Pachydactylus oculatus</i> | 1 | | |
| Scincidae | | | |
| <i>Mabuya</i> sp. (<i>varia</i> ?) | 1 | | |
| Chamaeleonidae | | | |
| <i>Bradypodion ventrale</i> | | 1 | Haagner & Branch 1993 |
| Agamidae | | | |
| <i>Agama aculeata distanti</i> | | 1 | Schmidt 1998 |
| Mammalia | | | |
| mouse <i>Leggaga bella</i> ? | | 1 | Loveridge 1933 |
| Total | 73 | 41+ | |

tain their sexual readiness throughout summer and autumn.

DIET

In total we obtained 73 prey items of which anurans were by far the most common (71 anuran prey items = 97%). The taxonomic diversity of the anuran prey items was large, with six families represented among the 51 anurans identified to family; however, bufonids (39%), ranids (29%) and microhylids (25%) comprised the bulk of the diet. The only two non-anuran prey items that we found were a gecko and a skink (Table 2). No tadpoles were found, indicating that only metamorphosed anurans are taken. There also has been a report of this species eating a sliced cow shin bone that was scavenged from a dog's bowl (Alexander, 1987). We did not detect any significant difference in the types of prey items taken by males vs females or adults vs juveniles. Bufonids, microhylids and ranids were represented in snakes of all ages and gender. Further, these three anuran families were represented in the diet during all months except July and August. Thus, these snakes feed all year except for mid-winter. The only major difference among snakes was in the size of prey items consumed.

Snake SVL and prey SVL were positively correlated ($r = 0.49$, $N = 23$, $P < 0.0183$; Fig. 4a) as were snake mass and prey mass ($r = 0.61$, $N = 22$, $P < 0.0026$; Fig. 4b). Small snakes tend to eat small anurans while larger snakes eat both small and large anurans. We did not detect any difference between the sexes in terms of prey weight relative to snake weight (slopes homogeneous $F_{1,8} = 0.09$, $P = 0.7716$; intercepts $F_{1,9} = 0.81$, $P < 0.4746$), prey SVL relative to snake SVL (slopes homogeneous $F_{1,8} = 0.59$, $P = 0.4653$; intercepts $F_{1,9} = 0.76$, $P < 0.4972$), or maximum prey width relative to snake head width (slopes homogeneous $F_{1,3} = 0.81$, $P = 0.4355$; intercepts $F_{1,4} = 1.96$, $P < 0.2557$).

DISCUSSION

In most of the attributes that we studied, *C. hotamboeia* is similar to many other snake species worldwide. For example, the vast majority of snake species attain relatively small body sizes (Pough 1980). Most species inhabit tropical to subtropical habitats (Vitt 1987), and a substantial proportion of them feed on anuran prey (Mushinsky 1987). They exhibit seasonally cyclic reproduction, with

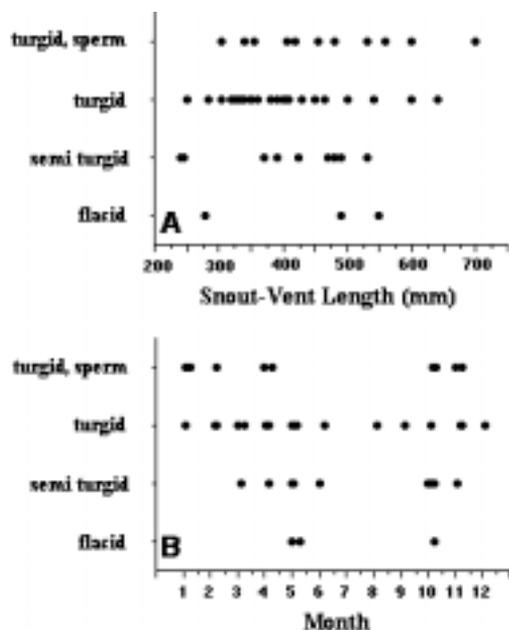


Figure 3. Reproductive biology of male *Crotaphopeltis hotamboeia*. The upper graph (A) shows that most males > 240 mm snout-vent length had turgid testes (indicating maturity), whereas the lower graph (B) shows that turgid testes were observed in specimens collected from virtually throughout the year.

oviposition in the warmest part of the year (Shine 1985). They reproduce by egg-laying, with the exact number of eggs depending on the body size of the female (Fitch 1970). Females attain larger body sizes than males, and have slightly larger heads at the same body sizes (Shine 1991, 1994). In all of these respects, *C. hotamboeia* is characteristic of the majority of snakes. Somewhat remarkably, however, snake species that display these common features have attracted much less scientific attention than have temperate-zone snakes with a different constellation of morphological and ecological traits. Because "typical" snakes such as *Crotaphopeltis* have (paradoxically) attracted relatively little detailed study, it is difficult to compare our data with that for closely related species. Nonetheless, a number of broad comparisons are possible (although many rely on anecdotal reports). As noted above, such comparisons generally reinforce the view that *C. hotamboeia* falls close to the average among

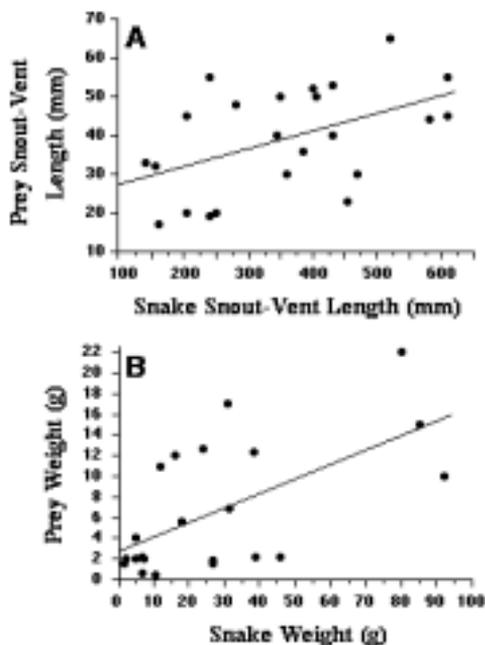


Figure 4. Predator-prey size relationships in *Crotaphopeltis hotamboeia* and their anuran prey. Larger snakes ate larger frogs, regardless of whether the comparison was based on snout-vent length (upper graph, A) or mass (lower graph, B). See text for statistical treatment of these data.

snakes for most of the traits that we have studied.

BODY SIZE AND SEXUAL DIMORPHISM

The largest male measured in this study (700 mm SVL) is the same specimen previously noted as being of record size (Haagner & Branch 1995). The largest female (830 mm SVL) exceeds the previous record size (790 mm, Broadley 1990). Using the calculation methods suggested by Gibbons & Lovich (1990), the degree of sexual size dimorphism in our sample of adult *C. hotamboeia* (Table 1) is 9.5% in favour of females. A recent review of 375 snake species revealed that females are on average 6.7% larger than conspecific males (Shine 1991). For 230 colubrid species within the same data set, the mean value was 8.5%. Our data on sexual dimorphism agree well with published literature. In terms of dimorphism in mean adult body size based on data in Broadley & Cock (1975), Fitch (1981) estimated SVL dimorphism to be 6.9% in favor of females in

C. hotamboeia. Measurements of preserved specimens in U.S. museums also enabled Shine (1991) to demonstrate significant sex divergence in relative head size in this species. As in our study, females had larger heads than males at the same SVL.

Our small data set does not allow us to clarify the ecological correlates of sexual dimorphism in body size and relative head size within *C. hotamboeia*, thus we can only speculate. Given that larger snakes eat larger prey (Fig. 4), it seems likely that the larger sex will on average consume larger prey. The head-size divergence might amplify this niche divergence, as it does in at least some other species (Houston & Shine 1993). However, the head-size divergence may have evolved for other reasons. For example, *C. hotamboeia* engages in a characteristic threat display that involves flattening of the head to such a degree that the vivid colouring of the lips can be seen from above (Broadley 1983). The relatively larger head of a female may thus allow for a more effective antipredator display. Alternatively, the head-size dimorphism between the sexes might have arisen as a phenotypically plastic response to sex-specific prey sizes, rather than as a genetically based adaptation (e.g., Queral-Regil & King 1998).

There is some confusion concerning hatchling size. FitzSimons (1962) records that hatchlings average 80 mm (about 4 inches) in total length. This mistake in metric conversion (4 inches = 100 mm) has been repeated in subsequent literature (e.g. Sweeney 1971; Broadley 1983; Pienaar *et al.* 1983). The smallest individuals measured during this survey had a TL of 142 mm. This corresponds to summarized records for hatchling size: 130-180 mm TL (Branch 1998), based on recorded measurements: 145-150 mm (Bogert 1940); 130 mm (Broadley & Cock 1975); 170-183 mm (Dyer 1982); 123 mm (Jacobsen 1989). The smallest wild-caught individuals recorded by Jacobsen (1989) were 111-118 mm. Four Gabon wild-caught specimens with obvious umbilical scars measured 151-172 mm TL (Branch unpubl. obs.).

REPRODUCTION

For such a relatively common and widespread snake, there are few detailed records of reproduction in *C. hotamboeia*. It appears to be similar to many other similar-sized snake species in its reproductive output, and our data support previous anecdotal records of reproductive seasonality and fecundity. Previous authors have recorded clutch sizes of 5 to 12 eggs, measuring 20.6-35 x 8-14.6 mm (e.g. Bogert 1940; Sweeney 1971; Pitman 1974; Dyer 1982; Jacobsen 1989; Broadley 1990). Clutches of 17 eggs have been recorded for snakes from Zimbabwe (Pitman 1974) and Mozambique (Manacas 1959).

The relatively long period over which females were found with oviductal eggs (October to January) suggests that individual females may be able to produce more than one clutch within a single year. However, we have no records of a female simultaneously containing oviductal eggs and vitellogenic follicles, so cannot speculate further on this point. Gravid females from East and Central Africa have been recorded from March (1 female), June (6 females) and December (2 females) (Loveridge 1936, 1942, 1953, 1955; Schmidt 1923), possibly indicating extended breeding in northern populations.

The fact that males appear to have sperm for much of the year suggests that mating may occur during autumn as well as spring, but again we have no direct evidence. The high reproductive frequency of adult females (which appear to reproduce each year) stands in strong contrast to the less-than-annual reproductive frequencies of females in many other snake species, including other taxa from southern Africa (e.g. *Bitis caudalis*: Shine *et al.* 1998). Presumably, the anurophagy and active-foraging habits of these small snakes allow them to obtain abundant food, while at the same time their small size makes them vulnerable to many sources of mortality. In combination, these traits are likely to favour a high allocation of energy to reproduction, rather than the low reproductive rates common in ambush-foraging species (e.g., Shine 1980; Greene 1997).

DIET

Our data on composition of the diet for *C. hotamboeia* are consistent with previous reports (Table 2). The only non-anuran prey types (apart from our own records) comprise four additional lizard species (two geckos, a chameleon and an agamid) as well as a single mouse (*Leggaga bella*). The claim that small snakes are included in the diet of Cameroon *C. hotamboeia* (Stucki-Stirn 1979) is without support. Dietary habits tend to be phylogenetically conservative among snakes, at least at the generic level (e.g., Greene 1997). In keeping with this generalisation, anurans appear to constitute the primary food items for all *Crotaphopeltis* species. Like *C. hotamboeia*, the pattern is that a very wide range of anuran species is consumed. For example, *Crotaphopeltis tornieri* has been recorded to consume *Callulina krefftii*, *Breviceps rugosus*, *Arthroleptis stenodactylus*, *Arthroleptis reichei*, *Probreviceps macrodactylus rungwenensis*, *Hyperolius puncticulatus*, *Leptopeltis ulugurensis* and *Phrynobatrachus ukingensis* (Rasmussen 1993). Anurans have also been reported in the diet of *Crotaphopeltis braestrupi* (Rasmussen 1985). Tadpoles have not been recorded in the diet of any *Crotaphopeltis*, and with few exceptions they feed mainly on terrestrial anurans, including many species with direct development (e.g. *Breviceps* and *Arthroleptis*). This prey spectrum indicates that *Crotaphopeltis* is not aquatic, but rather forages in mesic situations such as moist forest floors and among marginal vegetation.

In summary, our analysis of a large series of museum specimens of *C. hotamboeia* supports and extends previous anecdotal reports on the ecology and reproductive biology of these small riparian snakes. Inevitably, a study such as ours can only suggest directions for further research. Given their abundance and wide distribution, these small snakes would be well suited to more intensive ecological and behavioural studies.

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