Reproductive Biology and Food Habits of the Australian Elapid Snakes of the Genus Cryptophis

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ABSTRACT.—The two Cryptophis species are moderate-sized (up to 1 m length) nocturnal venomous snakes of northern and eastern Australia. Examination of 600 museum specimens provided data on body sizes, sexual size dimorphism, reproductive cycles and food habits. Males attain larger body sizes than females in C. nigrescens, but not in C. pallidiceps. Both species are viviparous, with a mean litter size of four. Parturition occurs in late summer (Feb.-Mar.) in southern populations, but may be earlier in snakes from tropical areas. Relative clutch mass averaged 60% in captive C. nigrescens, and offspring averaged 152 mm SVL and 2.3 g mass at birth. Male combat was recorded in C. nigrescens.

Both Cryptophis species feed on reptiles, especially scincid lizards (89% of all prey items found). A wide range of skinks is taken, but most are diurnally-active forms. Like many other Australian elapids, Cryptophis forage nocturnally for sleeping skinks. The absence of frogs from the diets of such elapids is a consistent but puzzling phenomenon. Relative eye size in Cryptophis is similar to that in other nocturnal elapids.

The proteroglyphous snakes of Australia are best-known for their highly toxic venoms; several of the large elapids are more deadly to man than are any snakes from other continents (Broad et al., 1979). However, these large and spectacular species constitute only a minor part of the radiation of the Elapidae in Australia. Most elapids are small and secretive; although they may be abundant, they have attracted little popular or scientific attention. The present study provides ecological data on such a group.

The genus Cryptophis contains two species, the eastern coastal C. nigrescens and the northern C. pallidiceps. Their phylogenetic affinities to other elapids are unclear. Cryptophis nigrescens attains moderate body lengths (up to 1 m), and is greyish-black dorsally and cream to pink ventrally. The head is small and the eyes reduced. The species is popularly known as the small-eyed snake. It is common in a wide variety of habitats, ranging from coastal heathlands to rainforests (Cogger, 1975). Specimens found during daylight hours usually are located in rock crevices (especially exfoliations) or under logs. These snakes move about actively at night, and I have noted activity also on overcast, stormy afternoons. Small-eyed snakes are very aggressive when aroused, and possess a toxic myolytic venom. One human fatality has been ascribed to the bite of this species (Pollit, 1981). Cryptophis pallidiceps closely resembles C. nigrescens, but is restricted to northern Australia. Like its southern congener, it is nocturnal and secretive in habit (Worrell, 1963; Gow, 1976).

MATERIALS AND METHODS

This study is based primarily on examination of 560 C. nigrescens and 40 C. pallidiceps in the collection of the Australian Museum, Queensland Museum, Northern Territory Museum, National Museum of Victoria and Australian National Wildlife Collection. Further data on C. nigrescens were obtained by collecting gravid snakes and maintaining them in the laboratory until parturition.

Preserved specimens in museum collections were first measured (snout-vent length, or SVL) and then a midventral
incision was made to determine (i) sex, (ii) maturity or immaturity (♀♀ were considered mature if they contained ovarian follicles >5 mm diameter, thickened oviducts or oviducal embryos; ♂♂ if testes were enlarged, or efferent ducts were thickened and opaque); (iii) identity of any prey items in the alimentary tract. In adult females, I also recorded litter sizes, and diameters of enlarged ovarian follicles. Adult female *C. pallidiceps* collected during the study were killed by nembutal injection and the oviducts dissected out and flushed with saline. This fluid was then examined microscopically for motile spermatozoa.

**RESULTS**

Sample sizes for *C. nigrescens* were large enough for separate analysis of populations in Victoria, New South Wales, and Queensland. Adults of both *Cryptophis* species average approximately 40 cm SVL (Table 1). Although male *C. nigrescens* consistently attain larger body sizes than females, the minimum size at sexual maturity (∼28 cm SVL) is similar in both sexes.

Viviparity (live-bearing) is the mode of reproduction of both the *Cryptophis* species. Gravid *C. nigrescens* containing full-term oviducal embryos were examined from Victoria, N.S.W. and Queensland. Captive females of this species from N.S.W. and southern Queensland gave birth in the laboratory. A single gravid female *C. pallidiceps* containing large oviducal embryos (Australian National Wildlife Collection #1529) confirms that this species is viviparous also.

Ovaries of adult female *C. nigrescens* contain small follicles for most of the year (Fig. 1). Vitellogenesis proceeds in spring, with ovulation in spring or early summer. The most common situation in southern (Victorian and N.S.W.) populations probably is ovulation in October or November and birth in February or March (Fig. 1, Table 2). However, northern Queensland *C. nigrescens* may ovulate earlier; three gravid females collected at Mount Molloy in November ranged from immediately post-ovulatory to full-term. Data on ovarian follicle diameters are less extensive for *C. pallidiceps*, but suggest a similar sea-

### Table 1. Sample sizes, body sizes and sexual dimorphism in body size of Cryptophis species. SVL = snout-vent length (cm).

<table>
<thead>
<tr>
<th></th>
<th>Victoria</th>
<th>N.S.W.</th>
<th>Queensland</th>
<th>C. pallidiceps</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Total sample size</strong></td>
<td>83</td>
<td>244</td>
<td>233</td>
<td>40</td>
</tr>
<tr>
<td><strong>Adult males</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sample size</td>
<td>31</td>
<td>82</td>
<td>68</td>
<td>21</td>
</tr>
<tr>
<td>$\bar{x}$ SVL ± SEM</td>
<td>38.9 ± 1.2</td>
<td>45.7 ± 1.1</td>
<td>49.0 ± 1.2</td>
<td>37.7 ± 1.5</td>
</tr>
<tr>
<td>SVL extremes</td>
<td>26.3-48.8</td>
<td>28.7-74.4</td>
<td>29.8-75.7</td>
<td>29.8-52.0</td>
</tr>
<tr>
<td><strong>Adult females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sample size</td>
<td>24</td>
<td>75</td>
<td>46</td>
<td>15</td>
</tr>
<tr>
<td>$\bar{x}$ SVL ± SEM</td>
<td>35.7 ± 0.7</td>
<td>35.6 ± 0.6</td>
<td>41.3 ± 0.9</td>
<td>42.7 ± 1.2</td>
</tr>
<tr>
<td>SVL extremes</td>
<td>28.5-41.8</td>
<td>30.0-48.1</td>
<td>29.3-71.0</td>
<td>36.5-54.0</td>
</tr>
<tr>
<td>Ratio $\bar{x}$ SVL ♂/♀</td>
<td>1.09</td>
<td>1.28</td>
<td>1.19</td>
<td>0.88</td>
</tr>
</tbody>
</table>
FIG. 1. Seasonal variation in diameter of the largest ovarian follicle in adult female *Cryptophis nigrescens*. Dots show follicle sizes, circles show diameters of oviducal “eggs” (i.e., embryos encapsulated in transparent membranes). Data for Victoria, New South Wales and Queensland combined.

seasonal timing to that of *C. nigrescens*. Diameters of ovarian follicles in adult female *C. pallidiceps* averaged 1 mm in January (N = 399), 2 mm in March (N = 1), 4 mm in May (N = 2), 4.2 mm in June (N = 4), and a single gravid female was recorded in October.

Thirty-four adult female *C. nigrescens* were collected during the time of year (Sept.-Dec.) when it was possible to classify them unambiguously as either reproductive (ovarian follicles >7 mm diameter) or non-reproductive (follicles <7 mm; Fig. 1). Twenty-six of these 34 females (76%) were in reproductive condition. Including data on reproduc-

<table>
<thead>
<tr>
<th>Litter #</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female SVL (cm)</td>
<td>39.6</td>
<td>35.1</td>
<td>42.5</td>
<td>36.2</td>
</tr>
<tr>
<td>Collection locality</td>
<td>Central coast of N.S.W.</td>
<td>Springbrook, Qld.</td>
<td>Mullumbimby, N.S.W.</td>
<td>Taree, N.S.W.</td>
</tr>
<tr>
<td>RCM</td>
<td>0.56</td>
<td>0.60</td>
<td>0.62</td>
<td>0.62</td>
</tr>
<tr>
<td>Litter size</td>
<td>5</td>
<td>4, + 1 infertile</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Neonatal SVL: mean (mm)</td>
<td>142</td>
<td>155</td>
<td>154</td>
<td>158</td>
</tr>
<tr>
<td>extremes (mm)</td>
<td>135-146</td>
<td>148-160</td>
<td>113-171</td>
<td>150-166</td>
</tr>
<tr>
<td>Neonatal weights: mean (g)</td>
<td>2.10</td>
<td>2.24</td>
<td>2.29</td>
<td>2.37</td>
</tr>
<tr>
<td>extremes (g)</td>
<td>2.0-2.2</td>
<td>2.2-2.4</td>
<td>0.8-2.8</td>
<td>2.3-2.4</td>
</tr>
</tbody>
</table>

| * Not recorded. |
tive females for which dates of collection were unknown, information on litter sizes was available for 33 female *C. nigrescens*. Probable litter sizes could be determined by counting enlarged ovarian follicles in a further 45 snakes of this species. Combining these data, fecundity ranges from one to eight offspring (Table 3). A mean litter size of approximately four characterizes female *C. nigrescens* from northern as well as southern populations. In the state for which the largest sample was available (N.S.W.), the correlation between maternal body length and fecundity was highly significant (P < 0.01, Table 3). Litter size in *C. pallidiceps* is similar to that in *C. nigrescens* (Table 3).

Female *C. nigrescens* maintained in captivity provided detailed data on parturition times, sizes of neonates, and maternal weight loss at parturition (Table 2). Offspring averaged 152 mm SVL and 2.3 g in mass at birth. Sizes of neonatal *C. pallidiceps* are unknown; judging by the embryos in the single gravid female examined, they are likely to be of similar size to *C. nigrescens* offspring.

No field data are available on mating activity, although I found a mature male and female *C. nigrescens* together under a single rock at Colo Heights (near Sydney) in November 1981. Neil Charles (pers. comm.) observed combat between two large (≈1 m total length) males near Springbrook, Qld., in October 1980. The snakes were intertwined on a blacktop road at approximately 2100 hours, on a warm night. He collected both snakes and confirmed their sexes by eversion of hemipenes. Four female *C. pallidiceps* collected near Darwin (Northern Territory) in June 1974 had abundant motile sperm in their oviducts. A male collected at the same time had the vas deferens packed with motile sperm.

Food habits of the two *Cryptophis* species are similar (Table 4). Of 111 prey items recorded, 99 (89%) were scincid lizards. Snakes (5%) were the only other significant category. Single records were obtained of an agamid lizard, a pygopodid lizard and two lizard eggs. No geckoes were recorded in gut contents. Only two frogs were recorded, and both of these were in the mouth (rather than the stomach) of the snake at the time of capture. Although the diet consists primarily of scincid lizards, a considerable diversity is present nonetheless. The skinks consumed include both small and large species (e.g., *Carlia*, *Tiliqua*), fossorial and surface-active forms (e.g., *Anomalopus*, *Ctenotus*) and nocturnal as well as diurnal lizards (e.g., *Sphenomorphus douglasi*, *Lampropholis*).

The sample size of *C. nigrescens* (560 snakes) is large enough for analysis of feeding rates. Eighty-four snakes (15%) contained prey items; these comprised 11% of the juvenile *C. nigrescens* collected, 15% of the adult males, and 21% of the adult females. This apparent ontogenetic and sexual variation in proportions of snakes with food differs significantly from the null expectation of equal proportions (N = 560, 2 df, $\chi^2 = 6.8, P < 0.05$). Data on *C. nigrescens* may also be analysed with respect to season-
al differences in feeding rates. The number of *C. nigrescens* collected in each month shows no significant variation between seasons (spring, summer, autumn, winter: $\chi^2 = 1.11, 3$ df, $P = 0.70$). The proportion of snakes containing prey items varies from 9% for snakes collected in autumn, to 19% for those collected in spring. However, these seasonal variations in apparent feeding rates do not attain statistical significance ($\chi^2 = 2.82, 3$ df, $P = 0.30$). Overall the data on *C. nigrescens* thus suggest differences in feeding rate associated with maturity and sex, but not with time of year.

**DISCUSSION**

*Cryptophis nigrescens* is similar to several other Australian elapid species in sexual dimorphism: males and females mature at similar SVLs, but males ulti-
mately attain larger body sizes (Shine 1978a). Samples of *C. pallidiceps* are too small for comparison (Table 1). Among snakes in general, large male size relative to female size correlates with the presence of male combat behavior (Shine, 1978b). In keeping with this correlation, male combat has been observed in *C. nigrescens*. The only other nocturnal elapid reported to show male combat is *Bungarus fasciatus*, an Asian krait (Taylor, 1965).

Data on Cryptophis reproduction presented in this paper are consistent with earlier anecdotal reports. *Cryptophis nigrescens* has long been known to be viviparous (Kinghorn, 1956; Worrell, 1963) but the mode of reproduction of *C. pallidiceps* has not been documented previously. Litter sizes of *C. nigrescens* reported by Worrell (1963) and McPhee (1979) fall within the range observed in the present study. Likewise, neonatal length has been reported at 13 cm (McPhee, 1979) and 10 to 12 cm (Gow, 1976), only slightly smaller than the mean SVL (15.2 cm) measured by me.

The food habits of Cryptophis appear to be less diverse than has previously been suggested. Both *Cryptophis* species feed primarily on scincid lizards (Table 4), and rarely (if at all) on frogs, geckoes or insects. These latter prey types have been suggested to be components of *Cryptophis* diets by most previous authors (Kinghorn, 1956; Rawlinson, 1965; Cogger, 1975; Gow, 1976; McPhee, 1979; but see Worrell, 1963; Jenkins and Bartell, 1980). The only specific records of prey items for *Cryptophis nigrescens* previously published are of an unidentified *Ramphotyphlops* (Covacevich and Ingram, 1975) and a *Ctenotus taeniolatus* (Rose, 1974). Both of these prey types were recorded in the present study also (Table 4). The validity of using museum specimens to determine feeding habits has recently been discussed (Shine, 1982).

Most prey items from Cryptophis are diurnally active reptiles (Table 4). Both *C. nigrescens* and *C. pallidiceps* are themselves nocturnal (Cogger, 1975), so I conclude that these snakes forage at night for inactive prey. Nocturnal foraging for inactive skinks is the main feeding “strategy” of small Australian elapid snakes of the genera *Cacophis, Furina, Glyphodon, Neelaps, Unechis* and some species within *Denisonia* and *Simoselaps* (Shine, 1980, 1981, 1983 and unpublished data). Frogs are rare or absent from the diets of all these snakes, despite being common in the habitats of many species. It is difficult to believe that frogs are not encountered by foraging snakes; I have found active *Cryptophis* at night on blacktop roads where frogs also were active. Both records of anuran prey in *Cryptophis* refer to frogs held in the snake’s mouth at the time of capture (Table 4), suggesting that these snakes occasionally seize frogs but do not swallow them. Studies on the toxicity of anuran skin secretions might clarify this problem.

Another puzzle in *Cryptophis* foraging is the adaptive significance of reduced eye size. *Cryptophis* is not exceptional in this respect, despite its common name of “small-eyed-snake.” Measurements of adult specimens in the Australian Museum show that eye diameter as a proportion of head length (snout to posterior edge of mandible) averages higher in *C. nigrescens* ($\bar{x} = 0.10$) than in *Glyphodon tristis* (0.08) or *Cacophis squamulosus* (0.08, $N = 10$ in each case). Fifteen other elapid species measured all have relative eye diameters greater than that of *Cryptophis*.

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elapids. The study was supported by the Australian Research Grants Scheme.

LITERATURE CITED


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