REPRODUCTIVE OUTPUT IN TWO SPECIES OF SMALL ELAPID SNAKES

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The front-fanged venomous snakes of Australia constitute a remarkable adaptive radiation of vertebrates: elapid species have evolved to occupy a wide variety of ecological niches in this country, and exhibit a correspondingly high diversity in body sizes, shapes and colours (e.g. McDowell 1985). Nonetheless, detailed information remains unavailable for many species. The most extensive information (and for many species, the only quantitative information) comes from examination and dissection of large numbers of preserved specimens in museums (see Appendix in Shine 1991). Although we can learn a great deal from this technique, there are many things that cannot be measured on preserved animals. For example, it is difficult to determine sizes at birth, dates of oviposition, hatching or birth, or reproductive output relative to the mother's body size. There is much current interest in the evolution of life-history “strategies” in reptiles, but information on Relative Clutch Mass (a measure of litter mass relative to the mother’s mass) is available for relatively few snake species (Seigel et al. 1986). During fieldwork in early summer 1994, we captured gravid specimens of two small elapid species. Because there are few detailed records of litter sizes, offspring sizes or Relative Clutch Mass for these common species, we kept these females in captivity until they gave birth. This paper describes the patterns of reproductive output that we recorded.

The two species are the Swamp Snake (Hemiaspis signata) and the White-lipped Snake (Drysdalia corniculata). The comparison between these two species is of particular interest, because they are similar in mean adult body sizes and in general appearance. Although previous phylogenetic work has not clearly resolved the relationships between these taxa, current work by one of us (JS Keogh) shows that the hemipenes of these two genera are very similar to each other, and quite different from those of any other Australian elapid snakes. Thus, it seems likely that Hemiaspis and Drysdalia form a natural (monophyletic) evolutionary lineage. Also, previous ecological work has shown a broad similarity between these two genera in diets (both feed on lizards and frogs) and reproductive cycles (Shine 1981, 1987).

The three White-lipped Snakes were collected on 5 December in the Brindabella Ranges, 40 km west of Canberra. The two Swamp Snakes were caught on 14 December near the Allyn River adjacent to Chichester State Forest in New South Wales. All of the females were maintained at the University of Sydney under natural day length. Hemiaspis females were housed in clear plastic boxes measuring 22 x 22 x 8 cm and Drysdalia females were housed in similar boxes measuring 22 x 13 x 8 cm. Topsoil was used as a substrate and one-half of each cage was heated with an underfloor heating coil so that the females could thermoregulate freely. Cages were checked daily and the females were weighed approximately every two weeks. As soon as we saw that birth had occurred, we weighed the female and weighed, measured and sexed her offspring. The females and babies were then preserved and deposited in the Australian Museum (registration numbers R147370 - 147399).

Table 1 provides the data on these females and their offspring. All gave birth over the period 8 - 28 February, in keeping with the reproductive timing previously inferred for these species (Shine 1981, 1987). Indeed, most viviparous temperate-zone Australian snakes seem to produce their offspring at about this time (Shine 1991). Perhaps the most impressive aspect was the high reproductive output relative to the mother's size in the White-lipped Snakes: Relative Clutch Mass (RCM_1) in Table 1) of this species averaged 1.02, indicating that the total mass of the litter (i.e., including fluids, membranes, etc. as well as the mass of the young weighed as much as the female did herself after giving birth (Table 1). RCM_1 was lower in the Swamp Snakes (mean = 0.42), although the small sample sizes mean that this difference between the species did not attain statistical significance (unpaired t = 2.16, 3 df, P = 0.12). RCM_2 was considerably lower than RCM_1.
(Table 1), indicating that much of the mass lost by the female at birth consisted of fluids, membranes, etc., rather than simply the mass of the offspring.

Table 1. Reproductive output in two species of small viviparous elapid snakes.

<table>
<thead>
<tr>
<th>Female #</th>
<th>SVL (mm)</th>
<th>Female mass before</th>
<th>Female mass after</th>
<th>Litter Size</th>
<th>Litter Mass (g)</th>
<th>RCM1</th>
<th>RCM2</th>
<th>Offspring Mass (g)</th>
<th>SVL (mm)</th>
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In most respects, the two species were quite similar. Litter sizes ranged from 5 to 6 in the White-lipped Snakes, and from 4 to 5 in the Swamp Snakes (unpaired \( t = 1.46, 3 \text{ df}, P = 0.24 \)). Offspring were larger at birth in Swamp Snakes (mean = 1.33 g, 133 mm SVL) than in White-lipped Snakes (0.90 g, 103.5 mm), but this difference between the two species was not significant once the variation among females within species was taken into account (two-factor nested analysis of variance with species, and female identification number nested within species, as the factors: species difference \( F_{1,20} = 4.42, P = 0.13 \) for mass, \( F_{1,20} = 6.06, P = 0.09 \) for SVL). Indeed, this variation among females within a species was quite marked: offspring from two of the White-lipped litters averaged 0.77 g (93 to 97 mm), whereas the offspring from the other litter were much larger (1.18 g, 121 mm). Average offspring sizes were more similar in the two Swamp Snake litters (1.4 and 1.2 g, 136 and 130 mm).
Two of the newborn Swamp Snakes were stillborn and could not be sexed with confidence. Of the
remainder, males outnumbered females among the captive-born offspring of both species (4 of 7
Swamp Snakes; 11 of 16 White-tipped Snakes). However, this bias was not statistically significant
in either case (chi-square test against a null hypothesis of 50% male: for Swamp Snakes, \( \chi^2 =
0.14, 1 \text{ df}, P = 0.70 \); for White-tipped Snakes, \( \chi^2 = 2.25, 1 \text{ df}, P = 0.12 \)). Sons and daughters did not
differ significantly in body sizes at birth in either species (White-tipped Snakes: \( F_{1,10} = 2.61, P =
0.14 \); Swamp Snakes, \( F_{1,4} = 0.003, P = 0.96 \)).

Our data are broadly consistent with earlier reports. The largest data sets on these species come
from Shine's (1981, 1987) examination of preserved specimens in museums, and from his
fieldwork on a population of \( H. \) signata in the New England highlands, near Armidale (Shine 1977a-c,
1978). Shine (1981) found that seven NSW \( D. \) coronoides had a mean clutch size of 6, their
neonates averaged 98 mm at birth, and their average RCM was 0.49. For \( H. \) signata,
Shine (1987) found that NSW females had a mean clutch size of 6.4 and two captive females gave
birth to young averaging 125 mm (1.33 g) and 127 mm (1.33 g), respectively.

Although museum specimens are important sources of otherwise hard-to-obtain biological data,
observations and measurements of live animals can give us information that we simply cannot get
from the museum specimens, e.g., on characteristics such as RCM. There is an important role
on traits of this kind (for examples see Bedford, 1992; Bush, 1992). We believe that it is useful to
know about differences in which these raw data can be used and analyzed. For example, there
are several different ways in which to calculate RCM. Because there is relatively little published
information on reproductive output in live Australian snakes, keeping and publishing accurate
reproductive data on captive snakes (including mass of the female as well as her offspring) can
provide a base for subsequent comparisons both within and among species.

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