

## Reproduction, Feeding and Growth in the Australian Burrowing Snake *Vermicella annulata*

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**ABSTRACT**—The Bandy-Bandy (*Vermicella annulata*) is a strikingly-colored (black-and-white-banded) fossorial elapid snake, widely distributed through Australia. Dissection of 276 museum specimens provided data on sexual size dimorphism, feeding habits, reproduction and inferred growth rates. Adult females ( $\bar{x}$  SVL = 54.4 cm) grow much larger than adult males ( $\bar{x}$  SVL = 39.2 cm). Typhlopids ("blind") snakes of the genus *Ramphotyphlops* were the only prey items found in *Vermicella* stomachs, and were the only prey types accepted by captive *Vermicella*. This stenophagy is unusual in Australian elapids. The low proportion of *Vermicella* containing prey items (1%, versus 20% in other elapids) suggests a low feeding rate in the Bandy-Bandy. The typhlopids consumed may often be larger than the *Vermicella* that eat them.

Vitellogenesis commences in October and eggs are laid in late summer (Feb.–Mar.) Clutch size ranges from 2 to 13 ( $\bar{x}$  = 7.7) and is highly correlated with maternal body length ( $P < .01$ ). Hatchlings are  $\approx$  17 cm SVL, and growth is slow. Sexual maturity is attained at  $\approx$  24 months in  $\sigma\sigma$ , but at least a year later in  $\text{♀♀}$ .

Behavior of captive specimens suggests that the banded coloration of *Vermicella* (i) is aposematic, and (ii) functions to confuse potential predators by creating a visual illusion (flicker fusion) when the snake moves rapidly. Attention is drawn to several Asian, African, American and Australian elapid species that show striking convergences with *Vermicella* in coloration, diet, behavior, morphology and general ecology. These aspects appear to be co-adapted, and result in a distinctive overall adaptive "strategy."

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### INTRODUCTION

The Bandy-Bandy (*Vermicella annulata*) is perhaps the most distinctive species among the entire radiation of elapid snakes in Australia. It differs from all other species in its spectacular coloration, dentition, and bizarre defensive display (Fig. 1). *V. annulata* is unusual also in its burrowing habits, virtually Australia-wide distribution, and specialized diet (see below). Taxonomically, *Vermicella* is only distantly related to other elapid genera (McDowell 1969). Apart from scattered anecdotal reports, nothing has been published on the ecology of this unusual species. The present study is based largely on dissection of museum specimens, and gives ecological information on eastern Australian populations of *V. annulata*. Data are provided on body sizes, sexual size dimorphism, food habits, seasonal reproductive timing, clutch sizes, inferred growth rates and ages at sexual maturity. Behavioral observations on captive snakes are also presented.

### MATERIALS AND METHODS

The Bandy-Bandy is a widely-distributed but rarely-encountered species. The geographic range of *V. annulata* extends over two-thirds of mainland Australia, with the species being absent only from southern Western Australia and the extreme south-eastern region of the continent (Cogger 1975). A northwestern congener, *V. multifasciata*, may not be sufficiently distinct from *V. annulata* to warrant specific status (Storr 1967). The coloration of the Bandy-Bandy consists of distinct alternate black-and-white rings along the body (Fig. 1). The dentition of this species is unusual in the

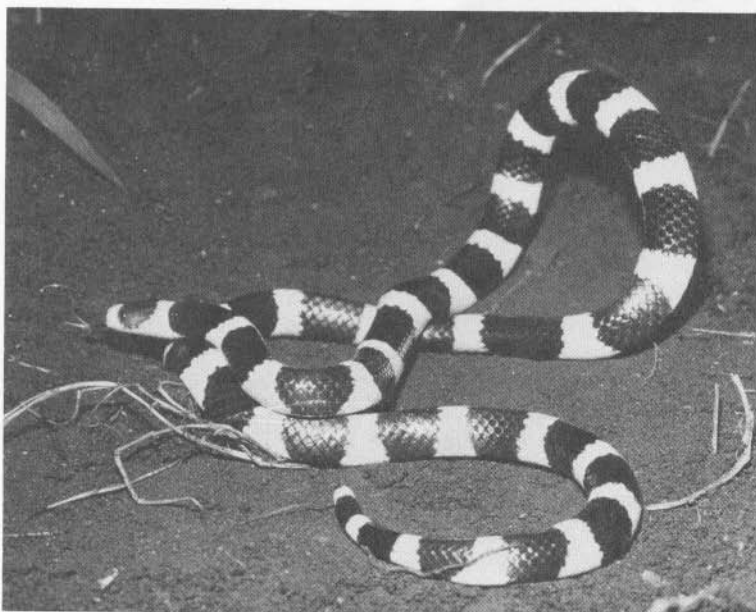


FIGURE 1. The Bandy-Bandy, *Vermicella annulata*, in defensive display. Note the raised body loop.

TABLE 1. Body sizes of *Vermicella annulata*. Table gives snout-vent lengths (SVLs) in cm.

	New South Wales	Queensland
Sample size (total)	133	135
<i>Adult males:</i>		
N	38	46
$\bar{x}$ SVL (& S.E.)	42.1 (1.0)	36.8 (.9)
range SVLs	29.0-52.6	28.2-53.4
<i>Adult females:</i>		
N	38	42
$\bar{x}$ SVL (& S.E.)	54.4 (1.5)	54.4 (1.2)
range SVLs	32.5-73.5	35.1-74.6

dimorphism. Females grow much larger than males in both populations (median test, 1 d.f.,  $P < 0.1$  in both cases), and also mature at larger sizes (Table 1).

(2) *Food habits.* Dissection of 276 preserved specimens yielded only three prey items from stomachs. All were typhlopids ("blind") snakes of the genus *Ramphotyphlops*, a group widely distributed over Australia (Cogger 1975). At least two of the three prey items were of the species *R. nigrescens*. Collection data for another Bandy-Bandy indicated that it had been found coiled up with a *Ramphotyphlops ligata*, presumably in the process of consuming the latter. In the three cases where blind snakes were found in *Vermicella* stomachs, the blind snakes were of approximately the same size (SVL) as the Bandy-Bandy. All four feeding records were from snakes collected in summer (November, December, January, March), and the four *Vermicella* were all large adult females.

presence of only a few small teeth following the fang (McDowell 1970). Collecting records and observations on captive snakes indicate that *V. annulata* is almost entirely nocturnal. When disturbed above-ground at night, captive specimens burrow rapidly into soft soil. Although venomous, the Bandy-Bandy rarely attempts to bite when handled. Instead, specimens assume a characteristic posture with a body coil lifted from the ground and held vertically (Bustard 1969; Fig. 1).

Most data in this paper were obtained from dissections of *V. annulata* in the collections of the Queensland Museum (Brisbane) and the Australian Museum (Sydney). The following measurements were taken: (i) snout-vent length (SVL), (ii) diameters of ovarian follicles or ovarian

eggs, (iii) gut contents, and (iv) reproductive maturity or immaturity (see Shine 1977a,b, for criteria). Growth rates were inferred from seasonal distributions of body size (see Shine 1978a).

## RESULTS

(1) *Body sizes.* Sample sizes, SVLs and sexual size dimorphism are described in Table 1. Northern (Queensland) and southern (New South Wales) populations do not differ significantly in body size or the direction of sexual

Two adult *Vermicella* were maintained in captivity individually for feeding trials. Both refused to eat (i) small elapid snakes of the species *Drysdalia coronoides*; (ii) burrowing skinks (*Hemiergis decresiensis*); and (iii) heliothermic skinks (*Lampropholis delicata*). A single large blind snake (*R. nigrescens*) was consumed < 6 hours after it was offered to one of the *Vermicella*. In conjunction with the dissection data, these results show that *Vermicella* feed primarily or exclusively on blind snakes of the genus *Ramphotyphlops*.

(3) *Reproduction*. Ovaries of adult female *Vermicella* are inactive over most of the year (Fig. 2). Enlarging ovarian follicles are seen in a few specimens in February ( $n = 2$ ), and June ( $n = 1$ ), but vitellogenesis is concentrated in October ( $n = 1$ ), November ( $n = 3$ ) and December ( $n = 3$ ). This latter period corresponds to late spring and early summer in eastern Australia. A single gravid female was recorded in February (late summer), and thick shells on her oviducal eggs indicate that this species is oviparous. The small diameter of oviducal eggs (22 mm) compared to ovarian follicles (up to 27 mm), as shown in Figure 2, reflects the great elongation of the pre-ovulatory follicles. Once ovulation has occurred, the eggs assume a more rounded shape.

Clutch sizes determined for 15 females ranged from 2 to 13 eggs, with a mean of 7.7 (S.E. = 0.78). Clutch size is highly correlated with female body size (Fig. 3; calculated regression, clutch size =  $.27 \cdot \text{SVL} - 6.78$ ), and there is no obvious geographic variation in clutch sizes (Fig. 3).

(4) *Seasonal abundance*. Snakes were collected in all months of the year (Fig. 4), but were less common in winter than in other seasons ( $n = 157$ , one-tailed  $\chi^2 = 2.9$ , 1 d.f.,  $P < .05$ ). Adult males and females show similar seasonal abundances ( $n = 100$ ,  $\chi^2 = 3.5$ , 3 d.f., n.s.), with most specimens being collected from late autumn to late summer (Fig. 4).

(5) *Growth rates*. Figure 5 shows the seasonal distribution of *Vermicella* body sizes. Hatchlings (SVL approx. 17 cm) appear in autumn, and growth appears to be slow during the first year of life. Great variability in the data make any conclusions tenuous, but I infer maturity (first mating) at about 24 months of age in male *Vermicella*, and at least a year later in females. These estimates are based on SVLs of the smallest mature specimens ( $\delta$ -enlarged testes, or sperm in efferent ducts;  $\text{♀}$ -ovarian follicles > 5 mm), combined with inferred growth rates from Fig. 5.

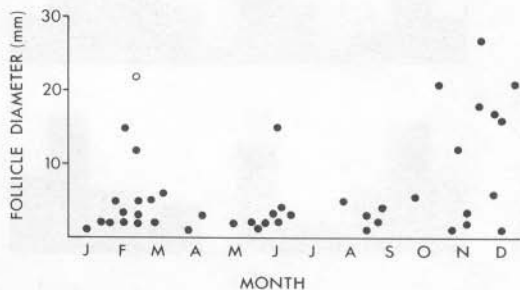


FIGURE 2. Seasonal variation in diameter of the largest ovarian follicle in adult female *Vermicella annulata*. Open circle = oviducal eggs.

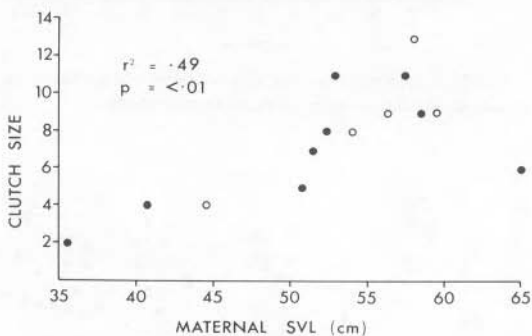


FIGURE 3. Relationship between maternal snout-vent length and clutch size in *Vermicella annulata*. Solid dots show Queensland snakes, circles show N.S.W. snakes.

## DISCUSSION

(1) *Sexual size dimorphism*. Females attain much larger body sizes than males in *Vermicella*, in contrast to most other elapid species for which data are available (Shine 1978b). Since male superiority in body size is highly associated with the presence of male "combat" behavior, I infer that such "combat" probably does not occur in male *Vermicella*. Large body size confers a considerable selective advantage in female Bandy-Bandies, because fecundity is highly size-dependent (Fig. 3).

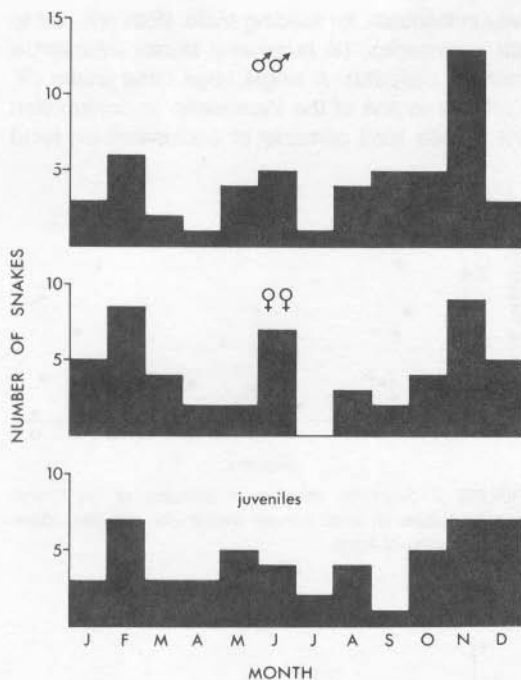


FIGURE 4. Seasonal abundances of *Vermicella annulata*, as shown by collection data for museum specimens.

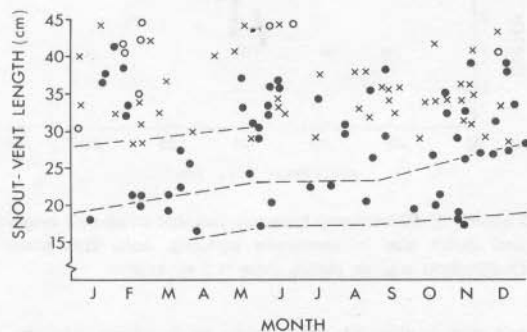


FIGURE 5. Seasonal distributions of body size, and inferred growth rates, in *Vermicella annulata*. Solid dots = juveniles; circles = mature ♀♀; crosses = mature ♂♂. Dashed line shows inferred growth pattern.

*Vermicella* dissected, only 1.1% contained prey. In contrast, dissections of 10 other elapid species in the same museum collections yielded an average of 20.3% of snakes with prey (range 11.3% to 27.3%). This difference in the incidence of prey items in *Vermicella* compared to the other species is highly significant ( $\chi^2 = 49.4$ , 1 d.f.,  $P < .01$ ). The difference cannot be attributed to (i) more rapid digestion in *Vermicella* (prey items are too large), or (ii) to differential capture of foraging (i.e. nonfed) specimens (since the same situation should apply with other nocturnal fossorial species, which are included in the above sample). I conclude that *Vermicella* feeds only rarely, a result consistent with the apparent low density and availability of their major prey type (*Ramphotyphlops*).

(3) *Reproduction*. The seasonal timing of reproduction in the Bandy-Bandy is similar to that seen in other Australian snakes (Shine 1977b). Observed clutch sizes (range 2 to 13, mean 7.7) are

(2) *Feeding habits*. The apparent specialization of *Vermicella*, feeding only on blind snakes (*Ramphotyphlops*), has been noted previously by Worrell (1963) and Cogger (1975). Other authors have included small burrowing skinks, as well as *Ramphotyphlops*, in the diet (McPhee 1959, Covacevich 1970, Gow 1976), although no specific data have been presented. Two further authors describe the *Vermicella* diet as "insects, frogs, small lizards and snakes" (Glauert 1957, Kinghorn 1964); this is certainly inaccurate. The results of the present study implicate *Ramphotyphlops* as the major food source of the Bandy-Bandy (see also Figure 2 in Kinghorn 1964), but I cannot dismiss the possibility that other items (e.g. small skinks) may also be taken. Although my own captive *Vermicella* refused to eat skinks (above), A. Taplin (pers. comm.) has recorded a captive *V. annulata* from northern Queensland feeding on the skink *Sphenomorphus punctulatus*. Further data on this point are needed.

The stenophagy of the Bandy-Bandy is surprising in view of the catholic food habits of most of the larger Australian elapids (Shine 1977c). It is tempting to speculate that the unusual dentition of *Vermicella*—only a few small teeth behind the fang (Krefft 1869, McDowell 1970)—is in some way an adaptation to feeding on typhlopids.

Another distinctive feature of the *Vermicella* diet is the large size of the prey items. Kinghorn's (1964) photograph of a dissected Bandy-Bandy containing a *Ramphotyphlops* offers an excellent example; the prey is much larger than the predator, and indeed protrudes for several cm out of the Bandy-Bandy's mouth. The same situation was seen in one of the *Vermicella* dissected in the present study. Presumably, this situation must continue until digestion is well advanced. Allied to the specialization of *Vermicella* on large rare prey items, is the apparently low frequency of feeding. Of 276 *Vermicella*



larger than have previously been suggested for this species. McPhee (1959) gave "three to six" as the usual clutch, while Gow (1976) believed that fecundity was  $\leq 6$  eggs. The observed relationship between fecundity and female body size (Fig. 3) is a common but not universal phenomenon in reptiles (Fitch 1970).

(4) *Growth Rates*. Hatchling size in this species has been variously reported as 13 cm (McPhee 1959), 17½ cm (Gow 1976), and 20 cm (Worrell 1964). The latter two estimates are probably the more accurate; the smallest field-collected individual in the present study was 17 cm SVL. Inferred growth rates of *Vermicella* (Fig. 5) are lower than in previously-studied elapids (Shine 1978a), perhaps because of the nature of the food resource. However, growth rates may be underestimated in the present study.

(5) *Overview*. This paper has stressed the unusual nature of *Vermicella annulata* in comparison with other Australian elapid snakes. In particular, I have emphasized the following array of characteristics: (i) brightly colored banded appearance; (ii) burrowing and nocturnal behaviors; (iii) unusual defence display (inoffensive, but showing "loop-raising"); and (iv) feeding mainly or exclusively on burrowing snakes. Have these characteristics evolved independently of each other, or are they all components of a single co-adapted "strategy?" If the latter interpretation is correct, one should find unrelated species showing convergences in all these features. A review of published literature offers support for this idea: banded, fossorial, nocturnal, snake-eating species have evolved independently several times within the family Elapidae (Table 2). The morphological, behavioral and ecological similarities between many of these species are remarkably close.

Why has natural selection favored such bright banding patterns? The two most probable hypotheses, which are not mutually exclusive, are (i) to "warn off" potential predators (all these

TABLE 2. Elapid snakes resembling *Vermicella annulata* in morphology (brightly banded color pattern), ecology and behavior.

Species	Locality	Burrow- ing ?	Noctur- nal ?	Ovipar- ous ?	Main Food Items	Defence Display	Authority
<i>Vermicella annulata</i>	Australia	✓	✓	✓	typhlopoid snakes	inoffensive; raising body loop	Present study
<i>Simoselaps bertholdi</i>	Australia	✓	✓	✓	burrowing lizards	inoffensive	Glauert 1957, Cogger 1975, Shine (unpubl.)
<i>Loveridgelaps elapoides</i>	Solomon Islands	✓	✓	?	typhlopoid snakes and skinks	inoffensive	McDowell 1970, M. McCoy (pers. comm.)
<i>Micrurus fulvius</i>	North America	✓	✓	✓	snakes, lizards	inoffensive; tail-waving	Wright & Wright 1957
<i>Micrurus</i> , 10 spp.	South America	✓	?	✓	snakes, lizards, amphisbaenids	?	Roze 1966, do Amaral 1977
<i>Micruroides euryxanthus</i>	North America	✓	✓	✓	leptotyphlopoid snakes	tail-waving cloacal popping	Stebbins 1966, Shaw & Campbell 1974
<i>Bungarus</i> , 3 spp.	Indo-China	✓	✓	✓	snakes, especially typhlopids in juveniles	inoffensive	Wall 1921, Smith 1943
<i>Callophis macclelandi</i>	Indo-China	✓	✓	✓	snakes, especially typhlopids	inoffensive	Wall 1921, Smith 1943, Whitaker 1976
<i>Aspidelaps lubricus</i>	Africa	✓	✓	?	snakes	hisses loudly	Fitzsimons 1962
<i>Elapsoidea semiannulata</i> (juv.)	Africa	✓	✓	✓	snakes	?	Broadley & Cock 1975
<i>E. sundevalli</i>	Africa	✓	✓	✓	insects	?	Fitzsimons 1962, 1974
<i>Elaps lacteus</i> (banded phase)	Africa	✓	?	✓	blind snakes & burrowing lizards	inoffensive	Fitzsimons 1962, 1974

snakes are venomous), and (ii) to "confuse" potential predators by producing a visual illusion (flicker fusion) that makes it difficult to locate a snake moving rapidly in dim light. Jackson et al. (1976) offer good empirical support for the latter hypothesis as a general explanation for banded color patterns in snakes. I have personally witnessed flicker fusion in captive *V. annulata*, and analysis of movie film shows that this species can greatly exceed the minimum "flicker frequencies" (number of bands moving past a given point per second) required to produce flicker fusion in dim light. The critical fusion frequencies (CFFs) of most vertebrate eyes range from about 10 to 50 cycles/second (Jackson et al., 1976), and analysis of film on two *V. annulata* in rapid flight revealed a range in flicker frequencies of 13.0 to 37.5 ( $n = 5$ ,  $\bar{x} = 23.6$ ) band cycles/second. These frequencies should exceed CFFs of most vertebrate eyes in dim light. The dependence of the flicker fusion phenomenon (in snakes) on low ambient light levels, offers an explanation for the common occurrence of the banded pattern in burrowing and nocturnal species (e.g. Table 2). Most potential predation on these species occurs under conditions of dim light.

It seems likely that the spectacular coloration of these species also pays an aposematic role, "warning" predators of the snake's venomous ability. This interpretation is consistent with the wide variety of bizarre defensive displays exhibited (e.g. tail-waving, cloacal popping, loop-raising—Table 2). It seems unlikely that these postures could deter predator attack unless the predator behaved as though the snake was dangerously venomous.

The general tendency for these banded burrowing snakes to be ophiophagous—and particularly to specialize on typhlopoid and leptotyphliid species (Table 2)—is more difficult to explain. It seems to be characteristic only of the elapids, for morphologically similar colubrid snakes (e.g. some members of the genera *Chilomeniscus*, *Chionactis*, *Cemophora*, *Gyalopion*, *Sonora*, *Lampropeltis*, *Erythrolampus*, *Pseudoboa*, *Lystrophis*, *Xenodon*, *Simophis* and *Telescopus*) take a much wider variety of invertebrate and vertebrate food items. Perhaps these differences reflect intercontinental differences in availability of different prey types (Shine 1977c).

Two other consistent features of the banded burrowing elapids are (i) "inoffensive" nature (reluctance to bite humans), and (ii) oviparity. I offer no explanation for the former, and the latter factor may simply reflect chance. However, the consistent correlations between the other factors listed above offer strong support for the co-evolution of morphology, ecology and behaviour in these burrowing elapids. Hence, the many unusual characteristics of *Vermicella* should be seen as a single co-adapted "strategy" rather than a suite of evolutionarily unrelated adaptations.

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