

Food Habits and Reproductive Biology of Australian Snakes of the Genus *Hemiaspis* (Elapidae)

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The genus *Hemiaspis* contains two species of proteroglyphous snakes: *H. damelii* of inland and near-coastal regions of central eastern Australia, and *H. signata* of near-coastal regions along most of the eastern Australian seaboard. Recent studies on karyology, immunology, electrophoresis and internal anatomy (Cogger, 1983; Mengden, 1985; Schwaner et al., 1985; Wallach, 1985) indicate that the two species are sister taxa, but their relationship is not particularly close. These data suggest a relatively ancient divergence within *Hemiaspis*, despite overall similarity in morphology, scalation and size in the two living species.

Previous work describes food habits, habitat utilization, and reproductive cycles in a geographically isolated population of *H. signata* near Armidale, N.S.W. (Shine, 1977a, b), and testicular cycles and inferred growth rates of both species of *Hemiaspis* (Shine, 1977c, 1978a). I here provide data on food habits and reproductive biology of *Hemiaspis*, based primarily on dissections of preserved specimens in museum collections. These data enable comparison of the two species of *Hemiaspis*, and also comparison of the Armidale population of *H. signata* previously studied with populations over the entire range of the species.

All preserved specimens of *Hemiaspis* in the collections of the Australian Museum, Queensland Museum, and Australian National Wildlife Collection

were examined, as were 55 specimens of *H. damelii* collected by me in central New South Wales (now in the Australian Museum). Preliminary information on testicular cycles and growth rates, based on these latter *H. damelii*, have already been published (Shine, 1977a, 1978a).

The following data were taken on 134 *H. damelii* and 367 *H. signata*: (i) snout-vent length (SVL); (ii) sex and reproductive condition (determined by dissection); (iii) maturity or immaturity (females were considered mature if they had ovarian follicles > 3 mm diameter, or thickened oviducts; males if testes were enlarged, or the vas deferens was thickened and opaque); (iv) in reproductive females, diameters of enlarged ovarian follicles, and litter sizes based on counts of these follicles or oviductal embryos; and (v) identity of any prey items in the stomach. Additional observations on feeding and reproduction were made on captive specimens.

The two species of *Hemiaspis* attain similar body sizes, averaging approximately 40 cm SVL (Table 1). Average body lengths are similar in northern (Queensland) and southern (N.S.W.) populations. Differences in size between the sexes are relatively minor, males averaging larger than females in *H. signata* but smaller in *H. damelii* (Table 1). However, this result for *H. damelii* is due mainly to the fact that males mature at slightly smaller body sizes than do females: the largest *H. damelii* recorded, both in Queensland and New South Wales, were males.

A total of 20 prey items was recorded for *H. damelii*, and 104 for *H. signata* (Table 2). The only invertebrate prey was a single large grasshopper in *H. signata*, possibly a secondarily ingested item (the same snake also contained a frog, *Litoria verreauxii*, in its stomach). All other prey items were lizards and frogs. Apart from one scincid lizard (unidentifiable to genus), all food items from *H. damelii* were anurans (Table 2). Of the 14 frogs identified to species, only two (*L. fallax*, *L. gracilentia*) are arboreal; the remainder are terrestrial. The diet of *H. signata* is much broader than that of *H. damelii*, with the recorded prey items including one invertebrate, 22 anurans, 68 lizards and 13 lizard eggs (Table 2). Only 2 of the 22 frogs are arboreal species. Apart from a single gecko, all of the lizards consumed by *H. signata* were skinks, with small diurnal species of the genus *Lampropholis* being the most important (37 records). The scincid species eaten also included fossorial (e.g., *Anomalopus*) as well as larger diurnal surface-active taxa (e.g., *Ctenotus*). Diets of Queensland and New South Wales specimens were similar in both species (Table 2). Observations of captive specimens supported inferences on dietary preferences from museum dissections. Captive *H. damelii* readily ate frogs, but not lizards or small mammals, whereas captive *H. signata* readily ate both frogs and lizards, but not small mammals.

The dissections of museum specimens also provided data on reproductive biology. Both species are viviparous (live-bearing), as evidenced by gravid females carrying full-term oviductal embryos. The seasonal timing of the female reproductive cycle can be inferred from variation in the diameter of ovarian follicles and the seasonal appearance of gravid females. In both Queensland and New South Wales

TABLE 1. Sample sizes, body lengths and sexual differences in body length in *Hemiaspis* species. SVL = snout-vent length (cm), N.S.W. = New South Wales, Qld = Queensland.

	<i>H. damelii</i>		<i>H. signata</i>	
	N.S.W.	Qld	N.S.W.	Qld
Total sample size	91	43	213	154
Adult males				
Sample size	39	17	85	38
\bar{x} SVL \pm SEM	42.6 \pm 1.3	37.8 \pm 2.0	39.0 \pm 1.1	42.7 \pm 1.7
SVL extremes	30.5-60.5	26.6-58.5	22.1-68.5	28.2-77.5
Adult females				
Sample size	22	12	70	57
\bar{x} SVL \pm SEM	46.3 \pm 1.5	40.1 \pm 1.1	35.8 \pm 0.8	39.3 \pm 0.9
SVL extremes	34.6-57.5	34.5-49.2	23.6-58.7	29.4-58.0
Ratio \bar{x} SVL δ/\varnothing	0.92	0.94	1.09	1.09

populations of *H. signata*, female reproduction is seasonal and synchronous (Fig. 1). Most gravid females (33 of 38 records) were collected from November to March (summer). Ovarian follicles are small (<5 mm diameter) for most of the year, but increase rapidly in size in spring (September-October), immediately prior to ovulation (Fig. 1). Fewer data are available for *H. damelii*, but the pattern is similar: five gravid females were collected, all in summer (December-February). Adult females (N = 8) examined from other months of the year had small (<5 mm) ovarian follicles. In both species, almost all adult-size females collected during summer (when they could be classified as either reproductive or non-reproductive) were either about to ovulate or gravid. Hence, the proportion of females reproducing each year is probably close to 100%.

Fecundity averaged higher in *H. damelii* (\bar{x} = 10.3, extremes 4-16, N = 8) than in populations of *H. signata* from either Queensland (\bar{x} = 7.7, 3-15, N = 27) or New South Wales (\bar{x} = 6.4, 3-15, N = 38). Litter size correlated significantly with maternal SVL in all samples: *H. damelii*, N = 7, r = 0.76, P < 0.05; Queensland *H. signata*, N = 27, r = 0.77, P < 0.01; New South Wales *H. signata*, N = 38, r = 0.66, P < 0.01. Hence, the higher fecundity of *H. damelii* is due at least partly to the larger average maternal SVL in this species (46.6 cm versus 38.7, 36.3 cm). Analysis of covariance of the relationship between litter size and maternal SVL showed no difference between the regression for *H. damelii* compared to *H. signata* from either Queensland (df = 1,31, C = 0.59, slopes F = 0.17, intercepts F = 0.72, n.s.) or New South Wales (df = 1,42, C = 0.71, slopes F = 2.24, intercepts F = 1.63, n.s.). However, the relationship between maternal SVL and litter size differed between Queensland and New South Wales specimens of *H. signata* (df = 1,61, C = 0.63, slopes F = 7.47, P < 0.05). This surprising result is due to a number of very small N.S.W. females with relatively large clutches, and some large females with small clutches. Hence, the slope of the SVL-fecundity regression was lower in the sample of *H. signata* from N.S.W. (0.23) than in that from Queensland (0.46).

Size at birth can be estimated from young born in the laboratory, from full-term oviductal embryos, or from the smallest field-collected animals. No births in captivity were recorded for *H. damelii*, so the only data available are a single full-term embryo of 14.5 cm SVL in a gravid female collected during parturition, and field-collected specimens of 12.8, 13.8, 14.0 and 14.5 cm SVL. Data are more extensive for *H. signata*. Two females from coastal New South Wales (Sydney region) gave birth in the laboratory, on 21 February 1981 and 31 January 1984. Six young from the first female averaged 12.5 cm SVL (range 11.7-12.8 cm) and 1.33 g (1.21-1.49 g), whereas three neonates from the second litter averaged 12.7 cm (11.0-13.9 cm) and 1.33 g (1.16-1.53 g). Offspring from two female *H. signata* from Queensland averaged 11.5 cm SVL (N = 15, SE = 0.11, 10.9-12.4 cm) and 12.6 cm SVL (N = 8, SE = 0.12, 12.2-13.2 cm). Full-term embryos of *H. signata* dissected from gravid females averaged 12.0 cm SVL (N = 14, SE = 0.16, 10.5-12.8 cm). The smallest field-collected *H. signata* was 10.7 cm SVL, with three others <11.0 cm, another six <12.0 cm, and another nine <13.0 cm SVL.

Data gathered in the present study are generally consistent with published information on the biology of *Hemiaspis*. The Armidale population of *H. signata* previously studied (Shine, 1977a, b, c, 1978a, 1979) conforms in most aspects of its ecology and reproductive biology to the patterns reported here. Additional prey types previously noted for *H. signata*, but not recorded in the present study, include tadpoles (Mackay, 1949; McPhee, 1959) and snakes (cannibalism: Holmes, 1955; McPhee, 1959).

Inevitably, a detailed comparison of the ecologies of two congeneric species will reveal both similarities and differences. The two *Hemiaspis* are similar in body sizes and in most aspects of reproductive biology investigated, but differ significantly in diets. The similarity in seasonal timing of reproduction in both taxa (Fig. 1) is not surprising, because all Australian temperate-zone snakes studied to date show this seasonal pattern (e.g., Shine, 1977b). However, other similarities are more significant: for example, the approximate equivalence in offspring sizes and in the

TABLE 2. Prey items identified from stomachs of *Hemiaspis* species, based on 20 prey items from 16 *H. damelii* and 104 prey items from 76 *H. signata*.

Prey item	<i>H. damelii</i>		<i>H. signata</i>	
	N.S.W.	Qld	N.S.W.	Qld
Invertebrates—grasshopper			1	
Frogs—unknown species				2
—Hylidae spp.	1	1	1	4
<i>Litoria alboguttatus</i>		1		
<i>L. bicolor</i>				1
<i>L. dentata</i>			1	
<i>L. fallax</i>		1		
<i>L. gracilentia</i>		1		
<i>L. verreauxii</i>			2	
<i>L. alboguttatus</i>		1		
—Myobatrachidae spp.	1	2	1	1
<i>Adelotus brevis</i>				1
<i>Limnodynastes</i> spp.			1	1
<i>L. fletcheri</i>	2			
<i>L. ornatus</i>		1		
<i>L. tasmaniensis</i>		1	2	1
<i>Ranidella signifera</i>			1	1
<i>Uperoleia</i> spp.		2	1	
Lizards—				
Scincidae spp.		1	16	6
<i>Anomalopus ophioscincus</i>				1
<i>Ctenotus</i> sp.			1	
<i>Hemiergus decresiensis</i>			1	
<i>Lampropholis</i> spp.			11	14
<i>L. challengerii</i>			3	1
<i>L. delicata</i>				4
<i>L. guichenoti</i>			1	2
<i>L. mustelina</i>			1	
<i>Leiopisma</i> sp.			1	
<i>Sphenomorphus</i> sp.			1	
<i>S. murrayi</i>			1	
<i>S. quoyii</i>			2	
eggs			7	6
Gekkonidae—				
<i>Phyllurus platurus</i>			1	

high proportions of adult females reproductive each year. The higher fecundity of *H. damelii* than *H. signata* is primarily due to larger average maternal body size in the former species, rather than to any species-specific adaptation of reproductive biology. A population of *H. signata* with an average maternal SVL similar to that of *H. damelii* also had litter sizes similar to those of *H. damelii* ($\bar{x} = 10.3$; Shine, 1977b). Similarly, the interspecific differences in sexual size dimorphism (Table 1) reflect minor differences in size (age?) at maturity: in both taxa, the largest specimens are males. Among snakes in general, males tend to grow larger than females only in those species in which males engage in combat bouts during the breeding season (Shine, 1978b). This correlation suggests that male *Hemiaspis* may show this behavior. Combat between two adult *H. signata* in Brisbane, Queensland, has been observed. Although the sexes of the snakes were not determined, the two snakes

were intertwined in typical combat postures (A. Easton, pers. comm.).

Dietary habits differ strikingly between the two species of *Hemiaspis*, with *H. signata* feeding on both lizards and frogs, and *H. damelii* restricted almost entirely to frogs. The virtual absence of lizards from the diet of *H. damelii* could be interpreted in two ways: either these snakes forage in places and at times such that they do not encounter lizards (or cannot catch them), or the snakes encounter lizards but do not attempt to eat them. Although lizards are abundant in many habitats frequented by *H. damelii*, it may be that *H. damelii* and *H. signata* differ in the times of day at which foraging occurs. In my experience in the Macquarie Marshes of central New South Wales, *H. damelii* is exclusively crepuscular: snakes begin moving about at sunset, but are active for only one or two hours after that time. In contrast, *H. signata* may be found active throughout the day as well

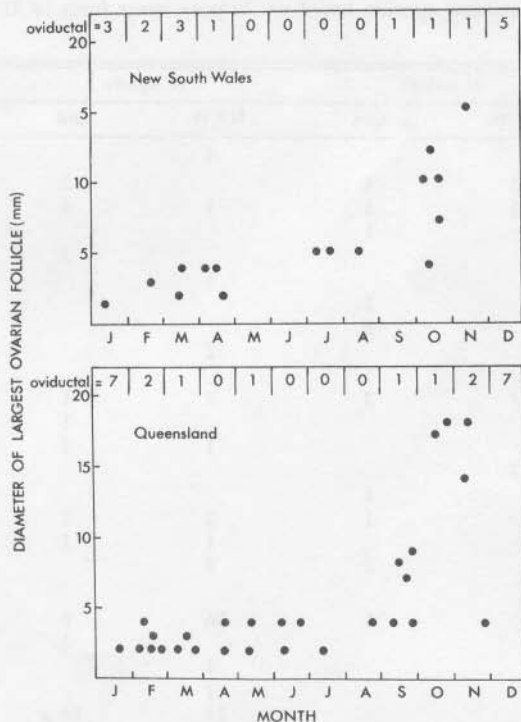


FIG. 1. Seasonal variation in diameter of the largest ovarian follicle in adult female *Hemiaspis signata* from eastern Australia. Numbers of females with oviductal young recorded in each month are indicated at the top of each graph.

as in the evening (to 2100 h; Shine, 1979). The crepuscular foraging of *H. damelii* may reduce its rate of encounter with potential lizard prey. However, the observation that lizards are not eaten by *H. damelii* even in captivity is more revealing. There may be a genetically-based difference between the two species of *Hemiaspis* in their willingness to eat lizards (c.f. Burghardt, 1967), but the selective advantage of such innate stenophagy versus euryphagy is unclear.

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