Journal of Herpetology, Vol. 17, No. 2, pp. 171-175, 1983

Food Habits and Reproductive Biology of Australian Elapid Snakes of the Genus *Denisonia*

RICHARD SHINE

Zoology A08, University of Sydney, NSW 2006, Australia

ABSTRACT. — The four species of *Denisonia* are small, heavy-bodied, nocturnal elapid snakes. Dissection of 414 museum specimens provided data on body sizes, reproductive cycles and food habits. All species attain similar body sizes (30-40 cm SVL), and sexual size dimorhpism is negligible. Litter sizes are low (4-7) and offspring measure approximately 12 cm SVL at birth. Two eastern Australian species (*devisi* and *maculata*) feed almost entirely on frogs, whereas the western species (*fasciata* and *punctata*) feed only on reptiles, especially agamid lizards. These differences probably reflect geographic differences in prey availability, but must also involve differences in foraging strategy: the western *Denisonia* feed on sleeping diurnal reptiles, whereas the eastern *denisonia* feed on active nocturnal animals. The east-west dichotomy is consistent with morphological data suggesting that the eastern and western species-pairs within "*Denisonia*" are only distantly related.

The proteroglyphous snakes of the family Elapidae have radiated widely on the Australian continent, so that Australian elapids are to be found in many different shapes, colors and sizes. Nonetheless, most species show the slender bodily form typical of elapids world-wide. The only notable exceptions are the heavy-bodied death adders (*Acanthophis*), bardicks (*Echiopsis*) and snakes of the genus *Denisonia.* The four species currently recognized in *Denisonia* (Cogger, 1975) are morphologically similar but occur in diverse habitats. Of the two eastern Australian species, *D. maculata* is restricted to forested areas of central eastern Queensland whereas *D. devisi* has a much larger range, in places extending into semi-arid regions of central Queensland and New South Wales. In contrast, the other two species, *D. fasciata* from Western Australia and *D. punctata* from the north-west are found in extremely arid regions (Smith, 1980). Apart from observations that all four *Denisonia* species are nocturnal (e.g., Worrell, 1963; Gow, 1976), little is known of the basic biology of these animals. The present study provides information on body sizes, sexual size dimorphism, food habits and reproductive cycles in the four *Denisonia* species.

MATERIALS AND METHODS

A total of 414 specimens were examined in the collections of the Australian Museum, Queensland Museum, Western Australian Museum and Australian National Wildlife Collection. After measuring snout–vent length (SVL), I made a midventral incision and recorded sex, and identified prey items and reproductive status. Males were considered mature if they had enlarged testes or opaque efferent ducts; females were considered mature if they had thickened oviducts, oviducal embryos, or ovarian follicles greater than 5 mm diameter. Diameter of the largest ovarian follicles, and clutch sizes were recorded in reproductive females.

RESULTS

Body sizes of all four *Denisonia* species are similar, averaging 30 to 40 cm SVL (Table 1). Adult males and females do not differ markedly in average body length, and sexual maturity is attained at similar body sizes in both sexes (Table 1). Specimens of *Denisonia devisi* from Queensland tend to be smaller than more southerly (New South Wales) snakes, but the difference is slight.

A total of 93 prey items were recorded

TABLE 1. Sample sizes, body lengths and sexual size dimorphism in *Denisonia* species. Snout-vent length (SVL) measurements in cm.

	devisi NSW	*devisi* Qld	*maculata*	*fasciata*	*punctata*
# of snakes examined	100	97	49	99	69
# of adult snakes	59	56	39	61	44
Adult males					
N	24	24	15	31	30
$\bar{x}$ SVL (SEM)	34.0 (0.8)	31.3 (0.7)	28.3 (0.6)	38.4 (1.4)	36.4 (1.0)
SVL extremes	27.7–46.3	24.4–38.7	23.0–31.3	28.4–51.3	25.6–50.2
Adult females					
N	35	32	24	30	14
$\bar{x}$ SVL (SEM)	36.1 (0.7)	32.1 (0.7)	33.5 (1.1)	38.7 (0.7)	34.2 (0.7)
SVL extremes	27.3–43.2	24.7–38.7	24.7–40.8	29.2–46.0	29.0–38.1
Ratio of mean SVL ♂/♀	0.94	0.98	0.84	0.99	1.06

from alimentary tracts. Of 414 snakes dissected, 77 (18.6%) contained prey. The lizards and frogs consumed by *Denisonia* covered a wide taxonomic range. Among the amphibians, both hylids and myobatrachids were commonly recorded (Table 2). Among the reptiles, agamid, gekkonid and scincid lizards all were noted frequently (Table 2). A clear dichotomy in diets is apparent, with the two eastern Australian species feeding mainly on frogs, and the two western species feeding on lizards (Table 2). Frogs comprised 88% of the diet (37 of 42 records) in *D. devisi* and 95% (17 of 18 records) in *D. maculata*, but were not recorded either in *D. fasciata* or in *D. punctata* (total of 33 records). The proportion of the diet comprised of amphibians was significantly different ($P < .01$) between *devisi* and *fasciata* ($\chi^2 = 33.9$), *devisi* and *punctata* ($\chi^2 = 27.7$), *maculata* and *fasciata* ($\chi^2 = 25.6$) and *mactulata* and *punctata* ($\chi^2 = 28.5$), but not different ($P > 0.20$) between *devisi* and *maculata* ($\chi^2 = 0.08$) or between *fasciata* and *punctata* ($\chi^2 = 0.00$).

Within the species *D. devisi*, a dietary difference was apparent between northern and southern populations. Four of the 16 prey recorded from Queensland snakes were lizards, whereas no lizards were recorded among the 26 prey items from New South Wales *D. devisi*. This difference is significant with a one-tailed test ($\chi^2 = 4.58$, 1 df, $P < .05$). These gekkonid prey from Queensland *D. devisi* are interesting because geckoes are only rarely taken by the lizard-eating western *Denisonia*. Hence, geckoes constituted a higher proportion of all lizard prey items in *D. devisi* (4 of 4 records) than in *D. fasciata* or *D. maculata* (total of 3 of 30 records) ($\chi^2 = 12.4$, 1 df, $P < .01$).

The dissection of museum specimens provided data also on reproduction. Viviparity (live-bearing) as the reproductive mode in *Denisonia* was confirmed by examination of gravid *D. devisi* and *D. punctata*. In both species, fully-developed young were seen in utero. No gravid females of *D. maculata* or *D. fasciata* were available.

The seasonal timing of the female reproductive cycle may be inferred from data on ovarian follicle sizes (Fig. 1). Ovaries of adult female *D. fasciata* contain medium-size (5–10 mm) follicles throughout the year, but major vitellogenesis and ovulation probably are restricted to spring (Sept.–Nov.). Fewer data are available for other species, but the same seasonal pattern is indicated in *D. punctata* (Fig. 1). Data for *D. devisi* and *D. maculata* are too scant to permit any conclusions.

Fecundity is low in all four *Denisonia* species, averaging from 3.7 in *D. punctata* to 6.8 in *D. maculata* (Table 3). There is no apparent correlation between female body length and fecundity intraspecifically (Table 3) or interspecifically (note that *D.*

TABLE 2. Prey items found in stomachs of *Denisonia* species.

	devisi NSW	*devisi* Qld	*maculata*	*fasciata*	*punctata*
# of snakes examined	100	97	49	99	69
# with identifiable prey	17	16	12	15	17
# of prey items recorded	26	16	18	15	18
Prey items					
Frogs—spp.*	3	2	4		
Cyclorana alboguttatus	1				
Litoria spp.*	2	2	2		
L. bicolor	10				
L. caerulea			1		
L. fallax			1		
L. latopalmata		1	1		
L. rubella	1				
Myobatrachid spp.*	4	1			
Limnodynastes fletcheri	1				
L. salmini	1				
L. tasmaniensis	1	3	6		
Neobatrachus spp.*	1				
Platypectron ornatus		2	3		
Uperoleia spp.*		1			
Lizards					
Agamid spp.*				6	5
Amphibolurus spp.*				1	
A. caudicinctus				2	
A. isolepis					1
A. reticulatus				1	
Diporiphora spp.*					2
Gekkonid spp.*		1		1	
Gehyra spp.*		3			
Oedura marmorata				1	
Rhynchoedura ornata					1
Scincid spp.*				2	6
Lerista bipes				1	
Snakes					
Ramphotyphlops spp.*					2
R. nigroterminatus					1
Insects					
Beetle			1		
Centipede	1				

* Unidentifiable to species level.

maculata has the smallest mean female SVL, but the highest mean fecundity). Offspring are large relative to adult body sizes. In *D. devisi,* full-term oviducal young averaged 11.5 and 10.6 cm in two gravid females, and the smallest specimen collected in the field measured 13.5 cm SVL. In *D. punctata,* full-term oviducal young averaged 11.9 and 12.3 cm SVL, and the smallest field-collected snake was 17.1 cm SVL. The smallest specimens recorded in the other two species were 14.1 cm SVL in *D. maculata* and 15.2 cm in *D. fasciata.* It seems likely that most *Denisonia* are born at approximately 12 cm SVL.

DISCUSSION

The data presented above may now be interpreted with respect to previously published information on *Denisonia* and on other Australian elapids. The approximate equivalence in mean adult body sizes of males and females is similar to the situation in several other small elapid

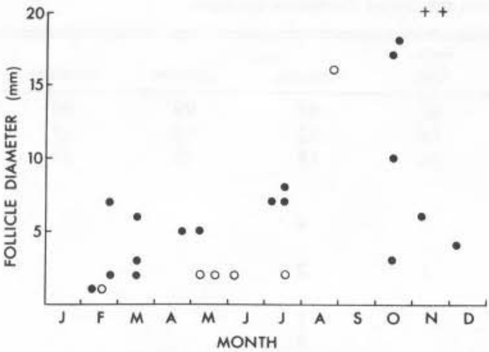

FIG. 1. Seasonal variation in diameter of the largest ovarian follicle in adult female *Denisonia fasciata* (dots) and *D. punctata* (circles). Crosses show oviducal embryos in *D. punctata*.

species (e.g., *Drysdalia, Echiopsis*—Shine, 1981*a*, 1982). This situation correlates with the presence of male combat behavior (Shine, 1978), but I have no reports of such behavior in any *Denisonia* species. This may simply reflect the dearth of field behavioral observations.

Several authors have commented on reproduction in *Denisonia*. Gow (1976) and McPhee (1979) noted that *D. devisi* is viviparous, with six to eight offspring. *D. maculata* has been recorded as producing eight to ten live-born young (Worrell, 1963; Kinghorn, 1964; Cogger, 1975; Gow, 1976). Bush (1981) suggested that *D. fasciata* is viviparous also, probably producing about five young. Gow (1976) recorded viviparity in *D. punctata*, with a litter size of five. All of these records are consistent with the results of the present study.

Published accounts of the food habits of *Denisonia* species are less reliable. Insects probably are a minor dietary item, rather than an important component as suggested by Glauert (1957) for *D. punctata* and Kinghorn (1964) for *D. maculata*. Both *D. maculata* and *D. devisi* feed almost entirely on frogs, not lizards (as in Cogger, 1975; McPhee, 1979; etc.). Specific gut-contents records of Glauert (1957) for *D. fasciata* ("a lizard") and Smith (1980) for *D. punctata* (*Amphibolurus, Diporiphora, Ramphotyphlops*) are based on specimens also examined in the present study. McPhee (1979) notes that *D. devisi* occasionally will feed on mice in captivity.

The dichotomy in diets between eastern and western *Denisonia* species is of particular interest. Why do *devisi* and *maculata* feed almost entirely on frogs, and *fasciata* and *punctata* on lizards? Part of the answer may lie with prey availability. Frogs are rare over much of the range of the western *Denisonia* (e.g., Tyler et al., 1981), whereas lizards, especially agamids, are common (Cogger and Heatwole, 1981). The reverse is true in the range of the eastern *Denisonia*. Similarly, the higher incidence of geckoes in the diet of northern versus southern populations of *D. devisi* simply may reflect the north-south cline in diversity and abundance of geckoes (Cogger and Heatwole, 1981).

Although the basic east-west dietary dichotomy may be due partly to prey availability, it must reflect differences in foraging mode as well. The eastern *Denisonia* feed on animals (frogs, geckoes) which are nocturnally active, whereas the western *Denisonia* feed on diurnal reptiles. All of the *Denisonia* species are themselves nocturnal (Worrell, 1963; Kinghorn, 1964; Cogger, 1975; Gow, 1976; McPhee, 1979; Bush, 1981). Hence, the western *Denisonia* must locate and consume sleeping (or at

TABLE 3. Fecundity of *Denisonia* species. SVL = snout-vent length (cm).

	Sample size	Mean SVL of adult ♀♀	Mean litter size	Extremes of litter size	Correlation coefficient between ♀ SVL and fecundity
D. devisi	14	34.2	4.93	3 to 9	−0.05 (ns)
D. maculata	5	33.5	6.80	3 to 11	0.55 (ns)
D. fasciata	13	38.7	4.31	2 to 7	0.28 (ns)
D. punctata	3	34.2	3.67	2 to 5	—

least inactive) lizards at night. This is a common foraging strategy in saurophagous Australian elapids (e.g., *Cacophis*, *Furina*—Shine, 1980, 1981*b*). In contrast, the eastern *Denisonia* species are active at the same time as their prey; presumably, frogs and geckoes are located while they are on their own foraging bouts at night. An alternative possibility is that the eastern *Denisonia* locate inactive individuals of their nocturnal prey species. If this were common, however, diurnal prey species also should appear in the snakes' diets; this does not occur (Table 2). I conclude that the western *Denisonia* species forage by searching for inactive prey, and that the eastern *Denisonia* feed on active nocturnal prey. Two different foraging modes are possible in the latter case: active searching, or "ambush" predation. Ambush predators such as vipers and death adders typically show a thickset body and broad head, as opposed to the more elongate morphology of "searching" foragers (e.g., Pough, 1979). In keeping with the hypothesized differences in foraging mode, the two eastern *Denisonia* species more closely resemble the typical "ambush" morphology than do their western congeners (see illustrations in Cogger, 1975). Field observations on *Denisonia* foraging would be of great interest.

McDowell (1970) suggested, on the basis of cranial musculature, that the western *Denisonia* were more closely related to the genera *Unechis* and *Suta* than they were to the eastern *Denisonia* species. Information on food habits supports this suggestion: not only do eastern and western *Denisonia* species differ in prey type and foraging modes, but the western species resemble *Unechis* and *Suta* in both respects (i.e., nocturnal snakes feeding on diurnal lizards; Shine, in prep.). Ecological data thus may aid in clarifying phylogenetic relationships, as well as illuminating some of the selective pressures involved in the evolutionary radiation of the Australian elapids.

Acknowledgments.—I thank G. Storr (Western Australian Museum), J. Covacevich (Queensland Museum), H. Cogger and A. Greer (Australian Museum) and J. Wombey (Australian National Wildlife Collection) for allowing me to examine specimens in their charge. The manuscript was expertly typed by T. Shine. The study was supported financially by the Australian Research Grants Scheme.

LITERATURE CITED

BUSH, B. 1981. Reptiles of the Kalgoorlie-Esperance region. Vanguard Press, Perth. 46 pp.

COGGER, H. G. 1975. Reptiles and amphibians of Australia. A. H. & A. W. Reed, Sydney. 584 pp.

———, AND H. HEATWOLE. 1981. The Australian reptiles: origins, biogeography, distribution patterns and island evolution. *In* A. Keast (ed.), Ecological Biogeography of Australia. Pp. 1333–1373. Junk, The Hague.

GLAUERT, L. 1957. A handbook of the snakes of Western Australia. W. A. Naturalists' Club, Perth. 62 pp.

GOW, G. F. 1976. Snakes of Australia. Angus and Robertson, Sydney. 88 pp.

KINGHORN, J. R. 1964. The snakes of Australia. Angus and Robertson, Sydney. 197 pp.

MCDOWELL, S. B. 1970. On the status and relationships of the Solomon Islands elapid snakes. J. Zool., Lond. 161:145–190.

MCPHEE, D. R. 1979. The observer's book of snakes and lizards of Australia. Methuen, Sydney. 157 pp.

POUGH, F. H. 1979. Modern reptiles. *In* W. N. McFarland, F. H. Pough, T. J. Cade, and J. B. Heiser, Vertebrate Life. Pp. 455–514. MacMillan, N.Y.

SHINE, R. 1978. Sexual size dimorphism and male combat in snakes. Oecologia (Berl.) 33:269–278.

SHINE, R. 1980. Comparative ecology of three Australian snake species of the genus *Cacophis* (Serpentes: Elapidae). Copeia 1980:831–838.

———. 1981*a*. Venomous snakes in cold climates: ecology of the Australian genus *Drysdalia* (Serpentes: Elapidae). Copeia 1981:14–25.

———. 1981*b*. Ecology of Australian elapid snakes of the genera *Furina* and *Glyphodon*. J. Herpetol. 15:219–224.

———. 1982. Ecology of the Australian elapid snake *Echiopsis curta*. J. Herpetol. 16:388–393.

SMITH, L. A. 1980. Taxonomy of *Denisonia punctata* and *Denisonia fasciata* (Serpentes: Elapidae). Rec. West. Aust. Mus. 8:327–333.

TYLER, M. J., G. F. WATSON, AND A. A. MARTIN. 1981. The Amphibia: diversity and distribution. *In* A. Keast (ed.), Ecological Biogeography of Australia. Pp. 1275–1302. Junk, The Hague.

WORRELL, E. 1963. Reptiles of Australia. Angus and Robertson, Sydney. 207 pp.

Accepted: 9 December 1982.