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Ecological Ramifications of Prey Size: Food Habits and Reproductive Biology of Australian Copperhead Snakes (*Austrelaps,* Elapidae)

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ABSTRACT.—Dissection of 641 specimens of three species of *Austrelaps* provided data on body sizes, sexual dimorphism, food habits, and reproductive biology. These snakes are large elapids of cool to cold climates in southeastern Australia.

Australian elapids mainly eat small prey, and foraging theory therefore predicts that they should be relatively unselective with respect to prey type and prey size. The diet of copperheads is very broad, including most of the locally available terrestrial vertebrates. Of 216 prey items, 66% were scincid lizards and 27% were frogs. Most prey items were very small, and there was no apparent relationship between prey and predator sizes. The proportion of snakes containing prey was consistently lower in juveniles than in adults, and lower in gravid females than in non-gravid females.

Austrelaps ramsayi and *A. superbus* are similar in body size, with *A. labialis* much smaller: all are similar ecologically. Males grow much larger than females, and are more numerous in museum collections. All three species are viviparous, with ovulation in spring and parturition in late summer. Only about two-thirds of adult-size females collected in summer were reproductive, suggesting that individual females may not reproduce every year. Litter sizes varied from 3 to 32, with means of 7.4 in *A. labialis,* 14.6 in *A. superbus,* and 15.0 in *A. ramsayi.* The lower fecundity in *A. labialis* is attributed to smaller maternal body size: the relationship between maternal SVL and litter size is similar among the three species. Size at birth is also similar.

Dietary specialization is more common in snakes than in other reptiles (Toft, 1985). Why is this so? Theory predicts that predators taking very few, large prey can more afford to turn down prey items and therefore reap the benefits of extreme food-type specialization (Schoener, 1974, 1977). Thus, the ability of snakes to subdue and consume very large prey may be a crucial factor allowing dietary specialization (Toft, 1985). In order to test this hypothesis, one needs to examine a group of snakes which do not eat large prey items: the clear prediction is that these animals should eat many different types of prey. Snakes which specialize on few, large prey are also likely to show selectivity with respect to prey size, such that larger snakes only eat the largest available prey (see Voris and Moffett, 1981, and Reynolds and Scott, 1982, for evidence of this phenomenon). In contrast, if there is no selective advantage to dietary specialization, a predator should consume prey of any size that it is capable of handling. If all prey items are small, the only difference between large and small predators would be that the larger animals would need to feed more often.

The venomous terrestrial snakes of Australia (family Elapidae) are an excellent example of a group in which most members feed on small rather than large prey, probably because the only commonly available prey in most Australian habitats are relatively small lizards and frogs (Shine, 1977*c*). The larger prey exploited by snakes of other continents, especially mammals, are rare in Australia (Shine, 1977*c*; Watts and Aslin, 1981). This scarcity of mammals is reflected both in a low species richness (Morton, 1979) and in low absolute abundances of most species except for the introduced house mouse (Morton and Baynes, 1985). A preliminary study of six species of elapid snakes in a montane region of eastern Australia (Shine, 1977*c*) suggested that they conformed to the predictions listed above: diets of most species were very broad, and even large snakes fed mainly on very small prey. The present study provides more extensive information on one of these genera: *Austrelaps*, the Australian copperheads. I examined specimens from throughout the geographic range of the genus to document food habits and reproductive biology. These data enable me to: (i) assess the degree to which the *Austrelaps* population previously studied is typical of the genus as a whole; and (ii) test the predictions of foraging theory outlined above.

Although some recent publications (e.g., Cogger, 1983) treat *Austrelaps* as a monotypic genus, at least three taxa can be distinguished on morphology (mainly labial coloration and numbers of ventral scales: Rawlinson, 1974 and pers. comm.). Published names are available for all three taxa, and two of these have been used recently by Sutherland (1983) on the basis of Rawlinson's findings. The taxa are: *Austrelaps ramsayi*, the highland copperhead of montane regions of New South Wales, extending into northern Victoria; *A. superbus*, the lowland copperhead, widely distributed in Victoria and Tasmania; and *A. "labialis,"* a pigmy form restricted to South Australia, in the Adelaide Hills, Kangaroo Island and adjacent mainland. Use of the name *A. labialis* is tentative because of slight uncertainty as to the identity of the type specimens (P. Rawlinson, pers. comm.). For detailed distribution maps of all three taxa see Sutherland (1983).

MATERIALS AND METHODS

All available preserved specimens of *Austrelaps* were examined from the collections of the National Museum of Victoria, the South Australian Museum, the Australian Museum and the Australian National Wildlife Collection. A total of 641 specimens was examined, consisting of 89 *A. labialis*, 248 *A. ramsayi*, and 304 *A. superbus*. This sample of *A. ramsayi* did not include 110 specimens collected in the Armidale region, for which ecological data have already been published (Shine, 1977*a*, *b*, *c*, 1978*a*, 1979, as "*A. superbus*").

For each specimen, I measured snout-vent length (SVL) and determined sex and reproductive condition through a midventral incision. Males were classified as mature if they had enlarged, turgid testes or opaque, thickened vasa deferentia. Females were classified as mature if they had ovarian follicles >5 mm diameter or thickened oviducts. Fecundity was determined from counts of enlarged ovarian follicles or oviductal embryos. Any food items in the stomach were removed, identified as far as possible, and measured. Data on dates and localities of collection were taken from museum registers.

RESULTS

A comparison of body sizes among sexes and species (Table 1) emphasizes the small size of *A. labialis* (ca. 45 cm SVL) compared to the other two species. Average body size of adult *A. ramsayi* and *A. superbus* was similar (about 75 cm SVL), and did not vary greatly among the different regions from

TABLE 1. Sample sizes and adult body lengths of *Austrelaps* species studied. SVL = snout-vent length (cm). SA = South Australia, NSW = New South Wales, Vic = Victoria, Tas = Tasmania.

	A. labialis	*A. ramsayi*		*A. superbus*	
	(SA)	(NSW)	(Vic)	(Vic, SA)	(Tas)
Total sample size	89	181	67	254	50
Adult males					
N	26	57	25	104	22
$\bar{x}$ SVL ± SE	48.4 ± 1.94	73.8 ± 1.85	73.9 ± 1.63	75.7 ± 1.32	80.5 ± 3.8
SVL extremes	30.5–75.5	44.6–103.0	58.8–89.4	47.7–122.0	52.7–124.5
Adult females					
N	34	33	10	56	13
$\bar{x}$ SVL ± SE	42.7 ± 1.22	63.7 ± 1.39	64.5 ± 2.26	66.8 ± 1.51	72.6 ± 1.86
SVL extremes	30.4–66.3	46.3–77.6	54.5–77.7	43.6–91.3	61.7–79.7
Ratio $\bar{x}$ SVL ♂/♀	1.13	1.16	1.15	1.13	1.11

which they were collected (Table 1). However, sexual differences in body size were extreme. In each sample, adult males attained much larger average and maximum body lengths than did females. Within each species, the size at which sexual maturity was attained was similar between males and females (Table 1).

Sex ratios of adult copperheads did not differ significantly from 1:1 for *A. labialis* (N = 60, 43% male, $\chi^2 = 1.07$, 1 df, n.s.), but were strongly skewed toward males both in *A. ramsayi* (N = 125, 67% male, $\chi^2 = 12.17$, 1 df, $P < 0.01$) and *A. superbus* (N = 195, 65% male, $\chi^2 = 16.67$, 1 df, $P < 0.01$).

A total of 216 prey items was identified from stomachs of 157 copperheads with prey (Appendix 1). These included 53 prey items from 42 *A. labialis*, 59 prey items from 49 *A. ramsayi* and 104 prey items from 70 *A. superbus*. Apart from three records of predation on invertebrates, three on mammals, one on a lizard egg and four on other snakes, all prey items identified from stomachs of *Austrelaps* were either lizards (N = 147) or frogs (N = 58). Although many different prey species were recorded within these categories, the overwhelming majority of lizards consumed (97%) were skinks. The frogs eaten were divided fairly evenly between myobatrachids ("ground frogs") and hylids ("tree frogs"), but by far the commonest prey item among the Hylidae was *Litoria verreauxii*, a terrestrial rather than arboreal species (Appendix 1). Although some *Austrelaps* reach large body size (Table 1), their prey are generally small (Appendix 1), and there is no apparent relationship between the size of the snake and the size of prey that it consumed, either in terms of mean prey SVL vs snake SVL (N = 77, $r = 0.07$, n.s.), or in minimum or maximum prey sizes vs snake SVL (Fig. 1).

The data may be analyzed with respect to the proportion of specimens containing prey items. Overall, the proportion of snakes with food items was higher in *A. labialis* (45%) than in either *A. ramsayi* or *A. superbus* (both 22%; $\chi^2 = 16.0$, 18.3, 1 df, $P < 0.001$ in both cases). Juveniles contained food less often than did adults both in *A. ramsayi* (12% vs 29%; $\chi^2 = 7.14$, 1 df, $P < 0.001$) and *A. superbus* (9% vs 29%; $\chi^2 = 16.0$, 1 df, $P < 0.001$). The same trend was evident in *A. labialis* (food in 30% of juveniles, 53% of adults), but was not statistically significant ($\chi^2 = 3.68$, 1 df, $P = 0.055$). There was no difference between adult males and non-gravid females in the proportions containing prey, whether by species (*labialis* $\chi^2 = 0.89$; *ramsayi* $\chi^2 = 0.80$; *superbus* $\chi^2 = 0.28$; 1 df, n.s.), or in all species combined ($\chi^2 = 0.48$, 1 df, $P = 0.49$). The proportion of adult females containing prey was consistently higher in non-gravid than in gravid specimens, but was not significantly different in any species, perhaps because of low sample sizes (*labialis*, 65% vs 44%, $\chi^2 = 0.74$, $P > 0.30$, *ramsayi*, 24% vs 0%, $\chi^2 = 2.78$, $P = 0.10$, and *superbus*, 26% vs 5%, $\chi^2 = 2.52$, $P = 0.11$). If

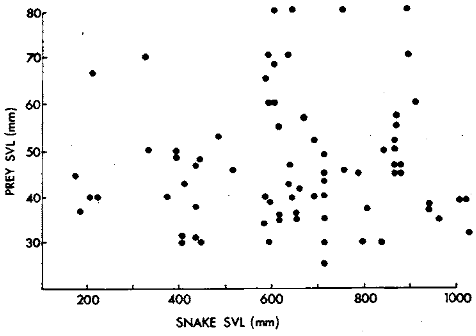

FIG. 1. Sizes of lizards consumed by *Austrelaps* in relation to the size of the snake.

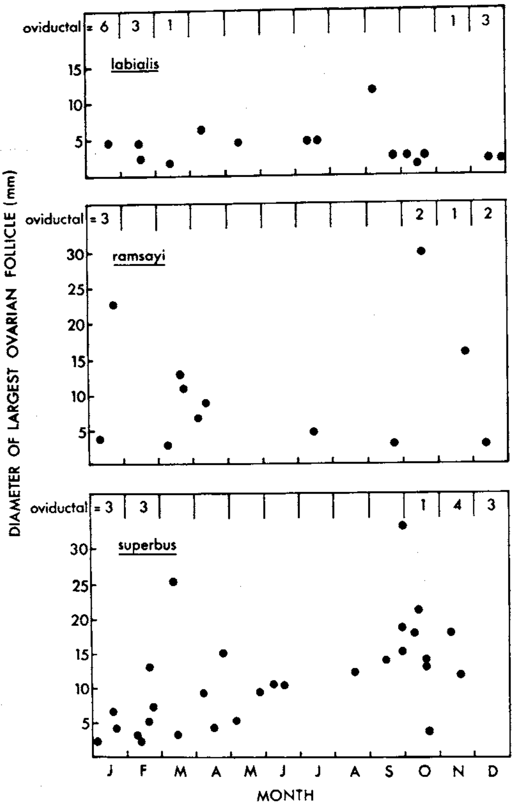

FIG. 2. Seasonal variation in diameter of the largest ovarian follicle, and in the number of gravid females collected, in three species of *Austrelaps*.

data from all three species are combined, the proportion of specimens containing food is significantly higher in non-gravid than in gravid snakes ($\chi^2 = 3.90$, 1 df, $P < 0.05$).

The proportion of snakes of each species (or sex, or reproductive status) containing lizards rather than frogs may be analyzed in a similar way. There is no indication of an ontogenetic shift in diet at this level of analysis: the relative numbers of lizards vs frogs found in stomachs did not differ between juvenile and adult *A. labialis* ($\chi^2 = 0.0$, 1 df, n.s.), *A. ramsayi* ($\chi^2 = 0.1$, 1 df, n.s.) or *A. superbus* ($\chi^2 = 0.5$, 1 df, n.s.). Among adult snakes only, dietary composition did not differ between males and females in a comparison combining all three species ($\chi^2 = 0.4$, 1 df, n.s.). The proportion of the diet composed of frogs vs lizards was also similar among the three species ($\chi^2 = 1.97$, 2 df, $P = 0.4$). However, if analysis is restricted to the two species occurring in Victoria, the diet of *A. ramsayi* in this state contained more lizards and fewer frogs than did the diet of *A. superbus* in the same state ($\chi^2 = 5.41$, 1 df, $P < 0.02$).

Museum records of collection dates for the dissected *Austrelaps* show strong seasonality, the total number of specimens per month varying from 11 in August (midwinter) to 78 in February (midsummer). The proportion collected in summer months is much higher than expected under the null hypothesis of equal numbers of snakes from each season ($N = 421$, $\chi^2 = 110.6$, 3 df, $P < 0.001$). The proportion of specimens containing food also shows seasonal variation (from 17% in winter to 30% in spring), but this variation is not statistically different from a null hypothesis of constant feeding rates among seasons ($\chi^2 = 5.2$, 3 df, $P = 0.16$).

Examination of museum specimens also provided information on reproductive biology. Gravid females with full-term oviductal embryos were observed in all three species, confirming that the reproductive mode is viviparity. The seasonal timing of the female reproductive cycle is similar in the three taxa, with all gravid females ($N = 36$) collected from late spring (October) to autumn (March). Adult-size females with inactive ovaries (largest ovarian follicles <5 mm), were recorded during summer in all species (Fig. 2), suggesting that females may not reproduce every year. The proportion of adult females that are reproductive can only be estimated from specimens collected during the time of year when it is possible to distinguish reproductive from non-reproductive snakes—that is, the summer months. Specimens collected prior to October may be wrongly classified as non-reproductive if they are simply delayed in vitellogenesis. Similarly, because parturition can occur as early as late February, post-parturient specimens collected after that time could also be wrongly classified as non-reproductive. Confining the sample to adult-size females collected from October to February (inclusive), the proportion of reproductive animals was 0.62 in *A. labialis* ($N = 21$), 0.59 in *A. ramsayi* ($N = 16$) and 0.59 in *A. superbus* ($N = 39$). These estimates are not significantly different from one another ($\chi^2 = 0.46$, 2 df, $P = 0.79$).

The estimates of reproductive frequency could be in error if mistakes were made in determining the minimum size at sexual maturity (Table 1): an underestimate of this variable would result in immature females being incorrectly classified as mature but non-reproductive. However, a comparison of body lengths of reproductive and non-reproductive females revealed no significant differences in mean female SVL between the two categories (*A. labialis*—reproductive $\bar{x} = 42.6$ cm, SD = 3.7, extremes 37.0–50.2 cm; non-reproductive $\bar{x} = 39.3$ cm, SD = 6.0, extremes 33.1–52.5 cm: *A. ramsayi*—reproductive $\bar{x} = 65.4$ cm, SD = 8.0, extremes 54.5–77.7 cm; non-reproductive $\bar{x} = 63.9$ cm, SD = 5.6, extremes 57.1–71.0 cm: *A. superbus*—reproductive $\bar{x} = 71.1$ cm, SD = 10.7, extremes 51.3–87.5 cm; non-reproductive $\bar{x} = 66.6$ cm, SD = 12.3, extremes 48.2–91.3 cm). This suggests that misclassification of immature animals is not a problem, and hence that only about two-thirds of adult female copperheads reproduce in any given year.

Information on litter sizes was obtained for 73 specimens of *Austrelaps*. Mean fecundity was significantly correlated with maternal SVL in *A. ramsayi* ($N = 21$, $r = 0.78$, $P < 0.01$) and *A. superbus* ($N = 36$, $r = 0.44$, $P < 0.01$), but not in *A. labialis* ($N = 16$, $r = 0.46$, $P = 0.06$), possibly because of the smaller sample size. Litter size ranged from three to 32 offspring, but was much lower in the pigmy copperhead ($\bar{x} = 7.4$) than in the two larger species ($\bar{x}$s = 14.6, 15.0). This apparent difference may be a simple consequence of the lower average maternal SVL in *A. labialis* (Table 3): analysis of covariance, comparing all three species, showed no significant interspecific differences in the relationship between fecundity and maternal SVL (slopes $F = 0.99$, df = 2, 67, n.s.; intercepts $F = 1.22$, df = 2, 69, n.s.).

Dissection of gravid females with full-term oviductal embryos also provided data on size at birth. These estimates can be compared to SVLs of the smallest field-collected specimens. Size at birth appears to be similar in all *Austrelaps*: full-term embryos averaged 13.1 cm and 14.4 cm SVL in two gravid *A. labialis*, 13.5 cm, 13.3 cm, and 14.2 cm in three *A. ramsayi*, and 16.8 cm in a gravid *A. superbus*. The smallest field-collected snakes were 12.9 cm SVL in *A. labialis*, 13.2 cm in *A. ramsayi*, and 11.9 cm in *A. superbus*.

DISCUSSION

The three species of *Austrelaps* are similar to each other, and to the single population of *A. ramsayi* previously studied, in most of the characteristics examined. The two larger species, *A. ramsayi* and *A. superbus*, are remarkably similar in body sizes, the degree of sexual size dimorphism, skewed sex ratios in collections, diets, litter sizes, reproductive frequencies and the proportion of specimens containing food. The pigmy copperhead (*A. labialis*) resembles the other species except in body size (and hence fecundity) and in the higher proportion of specimens containing prey.

The degree of difference in body size between males and females is greater in *Austrelaps* than in most other elapid snakes (e.g., Shine, 1977*a*, *b*). Larger size in males than in females generally occurs in species where rival males engage in vigorous physical combat (Shine, 1978*b*). Male combat has been reported in both the lowland copperhead, *A. superbus* (Shine and Allen, 1980) and the highland copperhead, *A. ramsayi* (J. Archibald, pers. comm.). The skewed sex ratios among adult *Austrelaps* in museum collections (Table 1) could be due either to an overproduction of males at birth (as in *Notechis scutatus*: Shine and Bull, 1977), or to differential behavior of the two sexes resulting in greater exposure of males to predation by humans.

The other main question raised in the Introduction concerns the degree to which the Australian elapids conform to predictions from foraging theory. In general, agreement is good. The prey eaten by *Austrelaps* are small, even in large snakes (Fig. 1), an inevitable consequence of the scarcity of large prey. Although there is a significant trend for larger prey in larger snakes, the slope of the relationship is low (0.02) and snake SVL explains little of the variance in prey SVL ($r^2 = 0.006$). Both the minimum and maximum prey sizes are almost independent of snake SVL (Fig. 1), suggesting that (i) small snakes are able to ingest even the largest available prey, and (ii) large snakes do not refuse small prey. I interpret this lack of correlation between snake size and prey size as a consequence of the generalized "searching" foraging of the snakes, combined with the scarcity of large prey. "Searching" foragers would be expected to consume all prey items encountered, even very small ones, because the costs of time, risk and energy to the snake of capturing and swallowing such prey are likely to be trivial (Schoener, 1972; Pough and Andrews, 1985). Hence, the only situation under which one would expect to see a relationship between snake size and prey size would be when some prey items were too large for ingestion by the smaller snakes. Large prey are rare in most *Austrelaps* habitats: the prey species listed in Appendix 1 include most of the commonly available species. Hence, all size classes of *Austrelaps* eat very small prey. Similar nonselectivity with respect to prey size has been reported in other elapid snakes, but in these cases some prey items have been too large for ingestion by the smallest snakes, resulting in an increase in maximum (but not minimum) prey size in larger specimens (Shine, 1977*c*; Greene, 1984).

Perhaps because of the restricted range of prey sizes, the frequency of feeding (as judged by the proportion of specimens containing food) is higher in adult snakes than in juveniles: presumably, larger snakes need more food. Field observations suggest that they are active searchers rather than ambush foragers, and this is supported by the nature of their prey (Appendix 1), including many amphibians which would presumably be in their diurnal retreats when found by the foraging snakes. It seems likely that *Austrelaps* capture these prey while foraging diurnally in crevices and under logs (Shine, pers. obs.). However, nocturnal activity has also been reported (White, 1981; Sutherland, 1983). The prey types and species utilized by *Austrelaps* are similar to those previously noted for *A. ramsayi* (Shine, 1977*c*). Most of the frogs consumed are terrestrial rather than arboreal species, and most of the lizards are diurnal surface-active taxa (Appendix 1).

The prediction of a generalized diet also is supported by these data. All of the commonly available potential prey types are eaten, and there is only minor variation in dietary composition among species, sexes or age groups. However, the proportions of specimens containing prey suggest variation in feeding rates depending upon the species, age and reproductive status of the snake. Differences in prey availability may be responsible for some of these trends: for example, the high proportion of *A. labialis* containing prey compared to the other species. The low proportion of gravid females containing prey is consistent with data on other snakes, including elapids (Shine, 1979, 1980), suggesting that females tend to reduce food intake during gestation.

As would be expected in snakes from cool climates, seasonality is evident in activity patterns (as judged by the numbers collected in each season), and in reproductive biology. Gestation occurs during the warmest months of the year, presumably allowing gravid females to maintain high body temperatures for embryonic development. The cool climate also may have played a role in favoring relatively low reproductive frequencies. Only about 63%

of adult-sized females collected during summer were reproductive, suggesting that individual females may skip reproduction every third year or so. The exact reproductive frequency probably depends on weather and on prey availability. A previous study found that the proportion of reproductive female *A. ramsayi* in northern New South Wales was 85% (Shine, 1977*b*), not significantly different from that of *A. ramsayi* in the present study (69%: $\chi^2 = 0.80$, 1 df, $P = 0.37$). Size at birth and litter size in relation to maternal body size are similar among the three *Austrelaps* species, and similar to data previously reported for *A. ramsayi* (Shine, 1978*a*).

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APPENDIX 1. Prey items identified from stomachs of *Austrelaps* species. Data for populations from New South Wales, Victoria and Tasmania given separately. "sp." = unidentifiable to species.

	A. labialis	*A. ramsayi*		*A. superbus*	
	(SA)	(NSW)	(Vic)	(Vic, SA)	(Tas)
Frogs—spp.	2	3	1	8	6
Myobatrachidae					
Limnodynastes sp.	1	1			
L. dumerilii		1		2	1
L. fletcheri	1				
L. peronii				1	
L. tasmaniensis				7	
Pseudophryne bibronii	3			1	
Ranidella signifera				2	
Hylidae					
Litoria sp.	1	1		3	
L. aurea				1	
L. citropa				1	
L. lesueuri			1		
L. peronii	1				
L. verreauxii		2			
Lizards					
Scincidae—spp.	5	3	2	8	1
Anotis maccoyi		2			
Ctenotus sp.		1			
Egernia saxatilis			1		
E. whitii		3			
Hemiergis decresiensis	1	1			
H. peronii	17			1	
Lampropholis sp.				3	
L. delicata				3	2
L. guichenoti	4	8	2	11	
L. mustelina		3	2		
Leiolopisma sp.				1	1
L. entrecasteauxii	5	3		4	6
L. metallicum					1
L. trilineatum			1	8	2
Lerista sp.	3				
Morethia adelaidensis	3			1	
Sphenomorphus sp.			5		
S. quoyii		2			
S. tympanum		1	5	6	
Tiliqua casurainae		1			
Gekkonidae					
Gehyra variegata	2				
Agamidae					
Amphibolurus diemensis					2
Lizard eggs	1				
Snakes					
Elapidae					
Austrelaps sp.		1		1	1
Drysdalia rhodogaster		1			
Mammals					
Mus musculus	1			2	
Insects					
Pupae	2				
Orthopteran		1			