

Arboreality in Snakes: Ecology of the Australian Elapid Genus *Hoplocephalus*

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Broad-headed snakes (*Hoplocephalus* spp.) are unusual among Australian elapids in being arboreal. Dissection of 332 specimens provided data on body sizes, sexual size dimorphism, food habits, reproductive cycles, fecundities and probable growth rates. Females grow larger than males in all three *Hoplocephalus* species. *H. bitorquatus* feeds mainly on arboreal pelodyadid frogs, *H. bungaroides* on lizards, and *H. stephensi* on lizards, mice and frogs. All species are viviparous, with ovulation occurring in late spring and birth in late summer. Young at birth are large (SVL 20 cm) relative to maternal size (SVL 50 to 70 cm), and litters are small (usually 4 to 6 young). Size-frequency distributions suggest sexual maturation at 3 to 4 years of age in *H. bitorquatus*. Most adult female *Hoplocephalus* reproduce only once every two years, or less often.

Compilation of published data on snake faunas of several continents reveals that a) food habits of arboreal and terrestrial snakes usually are similar; b) arboreality is more common in some taxonomic groups (e.g. colubrids) than in others (e.g. elapids); and c) the proportion of arboreal species in a snake fauna is highly correlated with annual precipitation. These findings may explain why arboreality is rare in Australian snakes.

DESPITE the wide adaptive radiation of elapid snakes in Australia, arboreality has evolved in only a few species (Cogger, 1967; Saint Girons, 1971; Heatwole et al., 1973). The only group consistently reported to be arboreal is *Hoplocephalus* (Cogger, 1967, 1975; Gow, 1976), a genus of three species restricted to eastern continental Australia. As is true for most Australian snakes, very little is known of the basic biology of these animals. Based on dissections of museum specimens, the present paper describes body sizes, sexual size dimorphism, food habits and reproductive cycles in *Hoplocephalus*. I briefly review published data on snake faunas of other continents to examine the degree to which the *Hoplocephalus* data show adaptations to arboreality.

MATERIALS AND METHODS

The present study is based on dissection of the following preserved specimens in the Queensland Museum (Brisbane) and the Australian Museum (Sydney): 215 *H. bitorquatus*, 52 *H. bungaroides*, 65 *H. stephensi*. Data taken were: a) snout-vent length (SVL); b) gut contents; c) sex; d) reproductive maturity or immaturity (criteria were: males—large testes or opaque efferent ducts; females—gravid, or ovarian follicles >5 mm); and e) diameters of ovarian fol-

licles or oviducal "eggs" (i.e., developing embryos encapsulated in clear membranes). I estimated growth rates in *H. bitorquatus* by analysing the body-size frequency distribution of snakes collected during cooler months of the year (May–September). By using data only from these months (when growth rates should be minimal) it was possible to tentatively infer age classes based on body size. Throughout the text, calculated means are followed by ± 1 standard error (SE).

RESULTS

The three *Hoplocephalus* species are morphologically similar. The body is long and fairly slender, and the head is broad and set off sharply from the neck (Fig. 1). All are chiefly nocturnal, although occasional specimens are seen basking during the day (N. Charles, pers. comm.). The degree to which these snakes are arboreal probably depends on the specific habitat; in some areas, all species may be found in rock crevices rather than in trees. Crevicedwelling is most common in *H. bungaroides*, whereas *H. bitorquatus* and *H. stephensi* are more consistently arboreal. All three species are restricted to relatively high-rainfall areas near the east coast, although *H. bitorquatus* also invades the drier eucalypt forests of the western slopes

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of NSW and inland Queensland. *H. bitorquatus* shows the widest latitudinal range—from northern Queensland to central New South Wales (NSW). *H. bungaroides* is restricted to a much smaller area in central and southern NSW, whereas *H. stephensi* occupies an intermediate area in northern NSW and southern Queensland (Cogger, 1975). All three *Hoplocephalus* species are renowned for their "nervous" temperament and willingness to bite. Their venoms are highly toxic but bites are usually not fatal to humans (Worrell, 1963; Cogger, 1975).

Body sizes.—Table 1 presents data on sample sizes of adult snakes, body lengths and sexual size dimorphism. *H. bitorquatus* is the smallest species and *H. stephensi* the largest. Specimens of *H. bitorquatus* from NSW tended to be larger than those from Queensland, but the difference was slight. Females attained much larger mean and maximum body sizes than males in all three species.

Food habits.—The three *Hoplocephalus* species differed in dietary habits (Table 2). *H. bitorquatus*, the smallest species, fed primarily on frogs (77% of the 26 prey items recorded), whereas *H. bungaroides* ate only lizards (N = 4). The larger *H. stephensi* ate lizards, mice and frogs. The lizards eaten include both nocturnal (e.g., gekkonid) and diurnal (mostly scincid and agamid) species. Relative to other lizards, geckoes appear to be a more important component of the diet in *H. bitorquatus* (3 of 4 records) than in either of the other *Hoplocephalus* (total of 1 of 8 records; Table 2). In the species for which the largest sample was available (*H. bitorquatus*), specimens containing prey items were collected in Feb., March, May, June, Oct. and Dec., suggesting that feeding occurs throughout the year.

Mode of reproduction.—Oviducal embryos were found in females of all three species, confirming that viviparity is the common reproductive mode.

Size at birth.—The smallest specimens measured were: *H. bitorquatus* 18.1 cm SVL; *H. bungaroides* 19.5 cm SVL; and *H. stephensi* 16.7 cm SVL. Three *H. stephensi* full-term embryos, still-born to a captive female, measured 16.7, 19.2 and 21.6 cm SVL (Queensland Museum records). Five neonatal *H. stephensi* measured 23 to 24 cm total length (L. Naylor, pers. comm.). Three full-term embryos of *H. bitorquatus* mea-

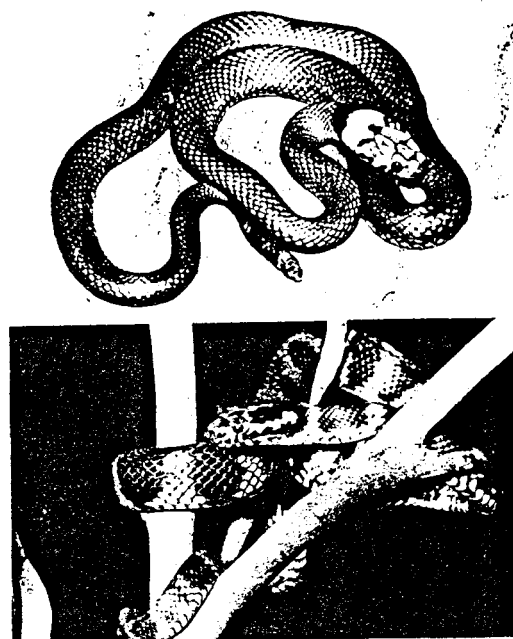


Fig. 1. Broad-headed snakes, *Hoplocephalus bitorquatus* (upper) and *H. stephensi* (lower). A truncated tail tip in the *H. bitorquatus* resulted from injury and is not typical. Photographs by A. Easton, Queensland Museum.

sured 19.5, 20.1 and 20.2 cm SVL. I conclude that size at birth is approximately 20 cm SVL in all three species.

Growth rates.—Fig. 2 shows the body-size distribution of *H. bitorquatus* collected during the cooler months of the year (May–Sept.). The rationale for this method is that growth rates should be low in cool weather, and the sample therefore approximates a sample taken at a single instant in time so far as growth rates are concerned. Fig. 2 reveals three distinct groups of immature snakes, with mean SVLs of 23, 31 and 37 cm respectively. I infer that the smallest size-class represents snakes in their first year of life, as birth occurs in Feb.–March at about 20 cm SVL. The next two peaks represent the next two year-classes. The largest immature snakes (SVL > 36 cm) may belong to the same year-class as the smallest mature animals, or maturity may be delayed for another year. Hence maturity probably is attained in either the third or fourth year of life (first ovulation at approximately 33 or 45 months of age) in *H. bitorquatus*.

TABLE 1. SAMPLE SIZES, ADULT BODY SIZES AND SEXUAL SIZE DIMORPHISM IN *Hoplocephalus* SPECIES. Snout-vent length (SVL) measured in cm.

	Species				
	<i>H. bitorquatus</i>			<i>H. bungaroides</i>	<i>H. stephensi</i>
	New South Wales	Queensland	Combined		
Adult males:					
Sample size	14	18	32	6	27
\bar{x} SVL \pm 1 SE	47.5 \pm 1.5	44.8 \pm 1.2	46.0 \pm 1.0	54.5 \pm 1.2	63.7 \pm 1.7
Range SVLs	37.6-57.2	36.2-53.5	36.2-57.2	50.9-58.5	47.9-79.5
Adult females:					
Sample size	20	47	67	15	23
\bar{x} SVL \pm 1 SE	55.6 \pm 2.2	51.0 \pm 1.3	52.4 \pm 1.1	57.2 \pm 2.1	69.4 \pm 1.4
Range SVLs	40.2-75.7	38.4-78.0	38.4-78.0	44.8-71.0	56.5-82.0
\bar{x} SVL ratio $\delta/\text{♀}$.85	.88	.88	.95	.92

Seasonal reproductive timing.—Data on female reproductive cycles are most complete for *H. bitorquatus*, although trends are similar in all three species (Fig. 3). Vitellogenesis commences during winter (May–July) and continues into spring. Ovulation occurs in late spring or early summer (Oct.–Dec.) and gestation continues through summer. Based on the seasonal appearance of newborn young in museum collections, births occur in Feb. and March. A captive *H. bitorquatus* gave birth in Feb. (N. Charles, pers. comm.). Mating in captive *H. stephensi* has been observed in Oct. (N. Charles, pers. comm.), and birth in late Dec. (L. Naylor, pers. comm.).

Many adult-size female *H. bitorquatus* had inactive ovaries (follicles < 5 mm) throughout the year (Fig. 3). A clear dichotomy in follicle size between reproductive and apparently non-reproductive females was evident for most of the year (April–Dec.). Of 26 females collected during this period, only 11 (42%) were reproductive. There was no significant differences in body sizes between reproductive and non-reproductive snakes (reproductive: $N = 11$, \bar{x} SVL = 49.6 \pm 2.0; non-reproductive: $N = 15$, \bar{x} = 52.1 \pm 2.5 cm). The proportion of reproducing females is low in the other species as well: 2 of 4 *H. bungaroides* and 2 of 7 *H. stephensi* females were reproductive.

Litter sizes.—In *H. bitorquatus*, litters of 17 females averaged 4.7 offspring, with a range in fecundity from 2 to 11. Litter size was highly correlated with maternal SVL ($r^2 = 0.70$, $P < 0.01$, \bar{x} ♀ SVL 51.2 cm). Two litters of *H. bun-*

garoides contained 4 and 8 offspring. Seven litters of *H. stephensi* averaged 5.7 offspring, with a range from 3 to 8. Litter size was highly correlated with maternal SVL ($r^2 = 0.50$, $P < 0.1$, \bar{x} ♀ SVL 68.6 cm).

DISCUSSION

This section first discusses the above data in the light of previous information on *Hoplocephalus*, and then considers some more general questions concerning arboreality in snakes.

Body sizes.—In the tendency for females to grow larger than males, *Hoplocephalus* resembles several other Australian elapid genera (*Acanthophis*, *Cacophis*, *Drysdalia*, *Furina*, *Neelaps*, *Simoselaps*, *Vermicella*) but differs from most of the larger species (*Austrelaps*, *Notechis*, *Oxyuranus*, *Pseudechis*, *Pseudonaja*—Shine, 1981a, b). No clear ecological correlates of the direction of sexual size dimorphism in these snakes may yet be drawn, except for the observation that male size superiority is most common in species in which rival males engage in combat bouts during the mating season (Shine, 1978). Male combat has never been recorded in *Hoplocephalus*, and would not be expected in view of the small size of males relative to females. It must be admitted, however, that even if these species do show male combat, it is unlikely that it would ever have been observed.

Food habits.—Published statements on the diet of *Hoplocephalus* are broadly consistent with the

TABLE 2. PREY ITEMS FOUND IN STOMACHS OF *Hoplocephalus* SNAKES.

Prey item	Snake species		
	<i>H. bitorquatus</i>	<i>H. bungaroides</i>	<i>H. stephensi</i>
<i>Lizards</i>			
Skinks—spp. unknown		1	
<i>Ctenotus taeniolatus</i>		1	
<i>Lampropholis guichenoti</i>	1		
<i>Sphenomorphus</i> spp.			1
Agamids spp. unknown			1
<i>Amphibolurus</i> spp.			1
<i>A. muricatus</i>		1	1
Geckoes—spp. unknown		1	
<i>Diplodactylus williamsii</i>	1		
<i>Gehyra</i> spp.	1		
<i>G. australis</i>	1		
<i>Frogs</i>			
spp. unknown	2		1
Pelodyadids—spp. unknown	10		
<i>Litoria caerulea</i>	2		
<i>L. rubella</i>	3		
Myobatrachids—spp. unknown	1		
<i>Limnodynastes fletcheri</i>	1		
<i>L. tasmaniensis</i>	1		
<i>Mammals</i>			
<i>Mus musculus</i>	2		4
TOTALS	26	4	9

results of the present study (Table 3). Further data on *H. bungaroides*, the least arboreal member of the genus, would be particularly valuable; Wells (1981) gives a recent summary of feeding records by captive snakes of this species.

Observations on captive specimens, and incidental field observations, suggest that all three *Hoplocephalus* species are strongly nocturnal. Hence, the diurnal prey items taken (*Ctenotus*, *Lampropholis*, *Amphibolurus*) may be consumed in their night-time retreats. Alternatively, these lizards might be taken during the day if they happened to venture under the same piece of cover as the snakes (Wells, 1981). Of the 20 frogs recorded in *H. bitorquatus* stomachs, at least 15 (75%) were tree-frogs (pelodyadids) rather than terrestrial species (myobatrachids). In contrast, Shine (1977) reported that diets in several terrestrial Australian snake species consist of myobatrachids at least as commonly as pelodyadids.

These data suggest—but do not demonstrate—that much of the foraging by *H. bitor-*

quatus occurs in trees. The proportion of frogs in the diet is much higher in *H. bitorquatus* than in the other two species; this difference may be related to the smaller body size of *H. bitorquatus*, or to the fact that it often occupies wetter areas than does *H. bungaroides* (Cogger, 1975).

Reproduction.—Hayes (1973) recorded mating in captive *Hoplocephalus* in March. My estimate for size at birth in *Hoplocephalus* (20 cm SVL) is close to previous reports. McPhee (1959) noted that *H. bungaroides* were 18 to 20 cm long at birth, and Gow (1976) recorded mean size in a captive brood of *H. stephensi* as 17.5 cm SVL. Gow's (1976) record of the litter size from this female (5 young) also is consistent with data from the present study. In contrast, the estimate of 20 young for *H. bungaroides* (McPhee, 1959; Cogger, 1975) is probably much too high. One probable reason for the low litter size in *Hoplocephalus* is the enormous size of the offspring (SVL ca. 20 cm) compared to the mother (SVL 50 to 70 cm).

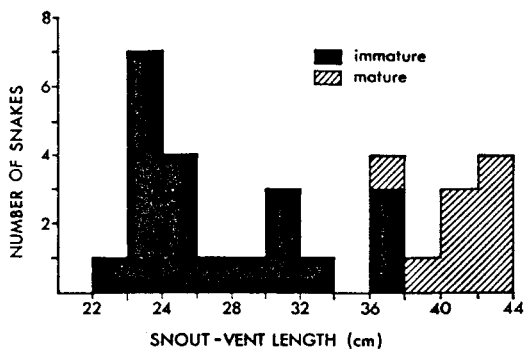


Fig. 2. Frequency distribution of body lengths of all *Hoplocephalus bitorquatus* collected during cool months of the year (May through September). Specimens greater than 44 cm SVL omitted.

One surprising finding is the observation that most mature-size female *Hoplocephalus* are non-reproductive (Fig. 3). This result cannot be due to mistakes in classifying juvenile females as "adult but non-reproductive", because the non-reproductive animals spanned the entire size range of reproductive females. Similarly, the high proportion of "non-reproducers" cannot be attributed to most specimens being collected in a few years that were unfavourable for reproduction, because the snakes examined were collected over a 90-year period. The only remaining explanation is that females of *H. bitorquatus* (and probably the other species as well) reproduce less often than annually. The data on ovarian follicle sizes for *H. bitorquatus* (Fig. 3) strongly suggest a "biennial" cycle (reproduction every second year, on average).

Such low frequencies of reproduction have been described in many ectothermic vertebrates, including several snake species (Bull and Shine, 1979). Apparently "biennial" female reproductive cycles recently have been reported in two other Australian elapids, *Acanthophis antarcticus* (Shine, 1980a) and *Drysdalia coronoides* (Shine, 1981a). Life-history theory predicts that low reproductive frequencies should evolve most often in species with a) "costs" of reproduction (lowered feeding or survivorship) that are relatively independent of fecundity; b) low rates of food intake, and c) high survivorship (Bull and Shine, 1979). A recent review suggests that "costs" of reproduction are widespread in reptiles (Shine, 1980b), although no specific data are available for *Hoplocephalus*. Feeding rates

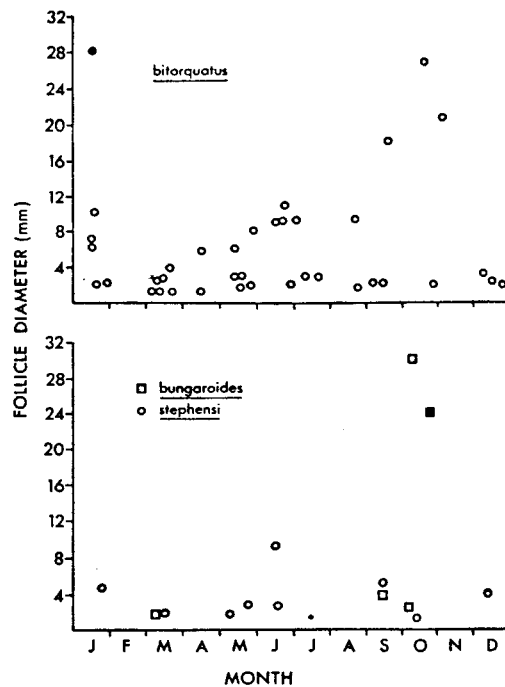


Fig. 3. Seasonal variation in diameter of the largest ovarian follicle (or membrane-encapsulated oviducal embryo) in *Hoplocephalus* species. Open symbols show ovarian follicles, solid symbols show oviducal "oocytes." Lower graph shows data for both *H. bungaroides* (squares) and *H. stephensi* (circles).

are unknown also, but the proportion of snakes containing food items was only 8% (*H. bungaroides*), 12% (*H. bitorquatus*) and 14% (*H. stephensi*). These percentages are similar to that (8%) seen in the biennially-reproducing *A. antarcticus* (Shine, 1980a). Other, presumably annually-reproducing elapid species in the same museum collections contain prey more frequently ($\bar{x} = 20\%$, $N = 10$ species—Shine, 1980a). A low rate of food consumption is often seen in captive *Hoplocephalus*, which remain inactive and hidden most of the time (N. Charles, pers. comm.). The final prediction from life-history theory is that *Hoplocephalus* should show high survivorship (Bull and Shine, 1979). Weak evidence supporting this prediction comes from the inactive and secretive nature of these snakes which should reduce exposure to predation. Also, the relatively late age at sexual maturation is consistent with high prereproductive survivorship (Williams, 1966).

TABLE 3. PUBLISHED DATA ON *Hoplocephalus* ECOLOGY.

Authority	<i>H. bitorquatus</i>	<i>H. bungaroides</i>	<i>H. stephensi</i>
(1) Diet			
Hosmer, 1952	—	lizards, birds, mice	—
McPhee, 1959	—	geckoes, skinks, mice	—
Worrell, 1963	—	skinks, geckoes, mice, birds, frogs	—
Kinghorn, 1964	—	lizards, mice	lizards, mice, birds, insects
Covacevich, 1970	frogs, lizards, birds, mammals	—	mammals, birds
Cogger, 1975	skinks	lizards, frogs	lizards, birds, mammals
Gow, 1976	geckoes, skinks	skinks, geckoes, mice, frogs	geckoes, skinks, mice, birds
Present study	frogs, geckoes	lizards	lizards, mice
(2) Fecundity			
Kreffit, 1869	2	—	—
McPhee, 1959	—	up to 20	—
Worrell, 1963	—	8	—
Cogger, 1975	—	8 to 20	—
Gow, 1976	—	6 to 8	5
Present study	2 to 11	4 to 8	3 to 8

Arboreality in snakes.—Several authors have commented on the low incidence of arboreal species among the Australian elapid fauna. Usually, *Hoplocephalus* is cited as the only arboreal genus (Cogger, 1967; Saint Girons, 1971; Heatwole et al., 1973). To what extent do my ecological data on *Hoplocephalus* show the effects of arboreality? An answer to this question requires knowing which ecological traits are characteristic of arboreal snakes as compared with terrestrial snakes on a world-wide basis. If consistent ecological differences between these groups are apparent, and if *Hoplocephalus* resembles arboreal rather than terrestrial species, then one may interpret these characters in *Hoplocephalus* as adaptations to arboreality. It seems clear that *Hoplocephalus* species show morphological features most common in arboreal snakes (e.g., slender body form, keeled ventral scales), and these may readily be attributed to selection for climbing ability. However, I know of no attempt to quantify overall ecological correlates of arboreality. Henderson and Binder (1980) have analysed morphological and ecological conver-

gences within a specialized guild of arboreal snakes.

One obvious ecological character in which arboreal and terrestrial snakes might differ is diet. A compilation of published data on snakes from Europe, Africa, Asia and South America provided dietary data for 221 terrestrial and 103 arboreal species (Wall, 1921; Pope, 1935; Minton, 1966; Pitman, 1974; Fitzsimons, 1974; do Amaral, 1976; Arnold and Burton, 1978). Many snakes were recorded to eat more than one type of prey. Results of this analysis show that arboreal and terrestrial snakes do not differ in the proportion of species feeding on amphibians (53% of arboreal species, 41% of terrestrial; $N = 324$, 2×2 contingency table, $\chi^2 = 3.76$, n.s.) or reptiles (65% of arboreal, 60% of terrestrial; $N = 324$, $\chi^2 = 0.51$, n.s.). However, birds (and their eggs) are a more important dietary component in arboreal species (eaten by 43%) than in terrestrial species (eaten by 18%; $N = 324$, $\chi^2 = 20.9$, $P < .01$). The reverse is true for mammals (arboreal 26%, terrestrial 52%; $N = 324$, $\chi^2 = 17.4$, $P < .01$). I suspect that the

apparently high incidence of bird-eating in arboreal snakes might not be supported by more detailed studies, because authors perhaps suggest that a snake preys on birds simply because the snake is arboreal. Whereas all three *Hoplocephalus* species have been reported to prey on birds (Table 3), I found no birds in stomachs. Overall, diets of arboreal and terrestrial snakes do not appear to be very different, at least on this superficial level. Reptiles, for example, are the most common prey type in both groups. Certainly, it is not possible to attribute any broad aspects of the *Hoplocephalus* diet to arboreality, except for the tendency of *H. bitorquatus* to take tree-frogs rather than ground-dwelling frogs. Adaptations of the diet to arboreality may best be looked for at this more detailed level, rather than searching for broad trends.

The suggestion that arboreality is unusually rare in Australian elapids (Cogger, 1967; Saint Girons, 1971; Heatwole et al., 1973) prompts another question: Why are there not more arboreal Australian species? To answer this question, one needs to investigate the factors which determine the incidence of arboreality among snake faunas in general. The two hypotheses which I will consider are that the proportion of arboreal species in an area may depend on a) environmental characteristics (especially vegetation), or b) the taxonomic composition of the snake fauna.

Consider the latter hypothesis first. If taxonomic composition is an important factor, then the proportion of arboreal species should be consistently higher in some families than others. My analysis of the data compiled for the discussion on diets (references above) shows that this is true. Some families (e.g., typhlopids, acrochordids) never show arboreality. Within the families containing arboreal forms, the proportion of species which are arboreal in each geographic region averaged .07 in elapids (data for 7 areas) and up to .22 in colubrids (8 areas). Other families are intermediate (.19 in boids, .13 in viperids). The difference between elapids and colubrids is significant (Wilcoxon's Rank-Sum Test, $N = 7, 8, W = 37, P < .03$). Hence, some geographic differences in the incidence of arboreality seem to be due to differences in the taxonomic composition of the snake fauna.

A more important factor is likely to be the environment, especially vegetational characteristics. If environment is important in determining the incidence of arboreality, then the proportion of arboreal species should be correlated

in different families of snakes occupying the same region. Analysis of the proportion of arboreal species in colubrid vs. non-colubrid snakes, across the eight different areas, confirms this prediction ($N = 8, r = .81, P < .01$). That is, areas with many arboreal colubrids also have many arboreal non-colubrids. The overall proportion of arboreal snakes in an area also is highly correlated with mean annual precipitation ($N = 8, r = .81, P < .01$), presumably because of the effect of precipitation on vegetation.

Results of these analyses may be applied to the Australian situation. The scarcity of arboreality in Australian snakes probably is a function both of environment (mainly arid) and of the taxonomic composition of the snake fauna (mainly elapids). In the entire Australian elapid radiation of 24 genera (Cogger, 1975), all are strictly terrestrial or fossorial except one or two genera. In contrast, the 8 genera of colubrids in Australia consist exclusively of arboreal and aquatic forms. An ecological comparison between Australia's arboreal elapids (*Hoplocephalus*) and colubrids (*Boiga*, *Dendrelaphis*) would be of great interest.

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