

Food Habits and Reproductive Biology of the Endemic Melanesian Elapids: Are Tropical Snakes Really Different?

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ABSTRACT.— Do the ecological traits of tropical snakes differ from those of temperate-zone species? We examined preserved specimens in museums to quantify body sizes, sexual dimorphism, dietary habits, and reproductive cycles of the proteroglyphous snake lineages endemic to New Guinea and the Solomon Islands for comparison with previously-studied Australian and Asian species. The Melanesian snakes comprise a diverse group in terms of body sizes (adult sizes from <50 cm to >1 meter), body shapes (slender to heavy-bodied), and behavior (nocturnal to diurnal). Males attain larger sizes than do females in *Aspidomorphus* and *Micropechis*, but the reverse is true in *Loveridgelaps*, *Salomonelaps*, and *Toxicocalamus*. *Aspidomorphus* and *Toxicocalamus* show significant sex differences in relative head length, but species in the other genera do not. All taxa for which we have data on reproductive mode are oviparous, and produce an average of 3 to 9 large eggs per clutch. Relative to maternal body sizes, Melanesian elapids have significantly smaller clutches than do Australian elapids. The two smaller-bodied genera showed dietary specialisation (on earthworms by *Toxicocalamus*, and on skinks by *Aspidomorphus*). *Toxicocalamus* and the Fijian *Ogmodon* are thus the only Old World elapids to specialise on invertebrate prey. The larger-bodied taxa (*Loveridgelaps*, *Micropechis*, *Salomonelaps*) have more generalised diets, consisting primarily of lizards and frogs. The distinctive features of the Melanesian elapid fauna (low fecundity in all taxa, and earthworm-eating by *Toxicocalamus*) may reflect adaptations to tropical habitats, but generalizations about the ecological adaptations of tropical snakes remain elusive.

A tropical animal may be exposed to very different selective pressures than its temperate-zone counterparts, because of distinctive features of climate, resource availability, interspecific competition, and predation in the tropics (e.g., Tinkle, 1969; Tinkle et al., 1970; Fitch, 1982). Hot conditions throughout the year may permit year-round activity, and hence accelerate growth rates and the attainment of sexual maturity (James and Shine, 1988). Expansion of the time period each year over which embryogenesis can proceed, may remove the main limiting factor that constrains reproductive activity to brief periods in most temperate-zone reptiles. The consequent potential for multiple-clutching may favor lower reproductive expenditure per clutch (Shine and Schwarzkopf, 1992). High species densities of potential prey types in tropical habitats may provide opportunities for dietary specialization in ways that are not possible in relatively species-poor temperate-zone habitats (Vitt, 1987). Available data tend to support these predictions: for example, clutches tend to be smaller, relative to maternal body size, in tropical lizards (Barbault, 1975; Rand, 1982; James and Shine, 1988) and snakes (Dunham et al., 1988; but see Aldridge et al., 1995).

Proteroglyphous venomous snakes ("elapids") are widespread in both marine and terrestrial habitats over most tropical and subtropical parts of the world. Detailed ecological information is available on some marine hydro-

phiids (Dunson and Minton, 1978; Voris and Jane, 1979; Voris et al., 1978) and laticaudids (Pernetta, 1977; Radcliffe and Chiszar, 1980) from the Pacific Ocean, and terrestrial taxa from North America (Jackson and Franz, 1981; Greene, 1984) and Australia (Shine, 1994a). However, ecological data are scarce for proteroglyphs from Central and South America, Africa, Asia, and Melanesia, despite the high diversity and abundance of elapid snakes in all of these regions. Available information on the ecological attributes of proteroglyphs from these areas (as for most tropical snakes) is based primarily on anecdotal reports, usually from regional faunal guides (e.g., Branch, 1988) or taxonomic revisions (e.g., McDowell, 1969, 1970, 1984). The ecology of tropical snakes remains virtually unknown, relative to the information available on temperate-zone taxa (Parker and Plummer, 1987).

The tropical oceanic islands lying to the north and east of Australia (New Guinea and the Solomon Islands, collectively called Melanesia) contain a diverse array of elapid species, which can be divided into two main groups (e.g., Cogger, 1971). The first group consists of Melanesian elapids that are closely related to (congeneric or conspecific with) Australian taxa (e.g., *Acanthophis*, *Demansia*, *Oxyuranus*, *Pseudonaja*, *Pseudechis*). Indeed, some species (e.g., *Pseudonaja textilis*) may have invaded New Guinea from Australia only recently, perhaps through direct

transport by human activities (Slater, 1956). The second group consists of Melanesian elapids which are more distantly related to Australian and Asian species. These include small cryptozoic taxa (*Aspidomorphus*, *Parapistocalamus*, and *Toxicocalamus*) as well as larger and more formidable snakes (*Loveridgelaps*, *Micropechis*, and *Salomonelaps*). The present paper focuses on representatives of these endemic Melanesian lineages, because these taxa are the ones that should show distinctive "tropical" characteristics, if indeed such characteristics exist. Our study is based primarily on our examination of preserved specimens in museum collections. We also review published literature on the ecology of these poorly-known snakes.

MATERIALS AND METHODS

We examined all available specimens of the endemic Melanesian elapids in the collections of the Australian Museum (Sydney), the South Australian Museum (Adelaide), the Bernice P. Bishop Museum (Honolulu), the California Academy of Sciences (San Francisco), and the Field Museum of Natural History (Chicago). Preserved snakes were first measured (snout-vent length, tail length, head length [along the lower jaw, from the tip of the snout to the quadrate-articular projection at the rear of the jaw], and head width [across the widest part of the head, between the two quadrates]). A midventral incision was made to reveal the gonads and alimentary tract, and we recorded sex and reproductive status. Males were scored as mature if they had large turgid testes and/or thickened opaque efferent ducts. Females were scored as mature if they had thick muscular oviducts, vitellogenic follicles, or oviductal eggs. In some poorly-preserved specimens, where the gonads were not distinguishable, we dissected the tail base and looked for hemipenes to determine sex. We opened both the stomach and the hindgut to search for prey items; any items found were removed for later identification.

Because of the paucity of information on most of these species, and the limited numbers of specimens in museum collections, we supplemented our museum data from two other sources. Firstly, we reviewed published literature to obtain records of ecological traits (especially, prey items or reproductive activity) in the endemic Melanesian elapids. Secondly, we corresponded with people who have first-hand experience with these species either in the field or in captivity.

RESULTS

(i) *Aspidomorphus* spp.—We obtained data on three species of small nocturnal elapids within this genus. Little seems to be known of the

natural history of these snakes. Parker (1982) noted that *A. muelleri* is a secretive terrestrial species, living in the forest under leaf litter and logs. McDowell (1967) suggested that the sexes of *A. lineaticollis* may differ in color, with a "concolor" morph apparently occurring only in males. In the same paper, he noted a strongly male-biased sex ratio in collections of *A. muelleri*. The same pattern was evident in our own data (Table 1). McDowell (1984) recorded a skink tail and a skink (*Sphenomorphus*) in stomachs of *A. lineaticollis*.

Our data show that males attain significantly larger body sizes than females in two of the *Aspidomorphus* species, and probably in the third as well (Table 1). For the two species for which sufficient sample sizes were available, we used heterogeneity of slopes tests and analyses of covariance to investigate whether males and females differ in shape (size of the head and tail relative to body length) as well as absolute size. For *A. lineaticollis*, these tests revealed that males had longer tails than did females at the same SVL (with sex as the factor and SVL as the covariate: slopes are homogeneous— $F_{1,21} = 0.34$, $P = 0.56$, but intercepts differ— $F_{1,22} = 22.1$, $P < 0.0001$; Fig. 1). Also, heads of males were both longer (slopes $F_{1,21} = 16.20$, $P < 0.0007$) and wider (slopes $F_{1,21} = 6.23$, $P < 0.022$) than were those of females at the same body length (Fig. 1). Head shape (length relative to width) did not differ between the sexes (slopes $F_{1,24} = 0.51$, $P = 0.48$; intercepts $F_{1,25} = 0.05$, $P = 0.83$). Sexual dimorphism in relative body proportions was less extreme in *A. muelleri*, but still statistically significant. At the same body lengths, males and females differed in tail length (slopes $F_{1,30} = 1.21$, $P = 0.28$; intercepts $F_{1,31} = 4.42$, $P < 0.05$), head length (slopes $F_{1,30} = 2.50$, $P = 0.12$; intercepts $F_{1,31} = 4.26$, $P < 0.05$) and head width (slopes $F_{1,30} = 2.31$, $P = 0.14$; intercepts $F_{1,31} = 5.81$, $P < 0.03$). As in *A. lineaticollis*, head shape (length relative to width) did not differ between the sexes (slopes $F_{1,33} = 0.12$, $P = 0.73$; intercepts $F_{1,34} = 0.49$, $P = 0.62$).

Gravid females of both *A. lineaticollis* and *A. muelleri* contained thick-shelled oviductal eggs, confirming oviparity in both taxa. Clutch sizes recorded in female *A. muelleri* ranged from three to five (mean = 3.5, SD = 0.84, N = 6) and were significantly correlated with maternal body size ($r = 0.88$, $P < 0.02$). Females of the smaller *A. lineaticollis* contained two to four eggs (mean = 2.71, SD = 0.95, N = 7), and clutch sizes were correlated with maternal body size in this species also ($r = 0.83$, $P < 0.021$). One female *A. schlegelii* contained two eggs, and another had three 20 mm ovarian follicles. Female *A. lineaticollis* with large (> 10 mm) vitellogenic ovarian follicles or oviductal eggs were collected in February, April, May, and August; reproductive *A.*

TABLE 1. Sample sizes, body sizes and sexual size dimorphism of six species of Melanesian elapid snakes, based on examination and dissection of museum specimens. SVL = snout-vent length, in mm. Last three columns show results from statistical tests for the presence of significant sexual dimorphism in mean adult body size.

	Adult males	Adult females	Unpaired t test		
			df	t	P
<i>Aspidomorphus lineaticollis</i>					
N	13	12			
Mean SVL (\pm SD)	412.8 (49.4)	349.5 (55.5)	23	3.01	0.006
Extremes	332-480	267-461			
<i>Aspidomorphus muelleri</i>					
N	20	12			
Mean SVL (\pm SD)	508.8 (66.0)	441.6 (63.6)	30	2.83	0.008
Extremes	347-620	344-542			
<i>Aspidomorphus schlegelii</i>					
N	1	4			
Mean SVL (\pm SD)	508	358.5 (53.0)	—	—	—
Extremes	—	296-405			
<i>Loveridgelaps elapoides</i>					
N	1	5			
Mean SVL (\pm SD)	670	1168.4 (160.8)	—	—	—
Extremes	—	990-1380			
<i>Micropechis ikaheka</i>					
N	23	19			
Mean SVL (\pm SD)	1025.0 (213.3)	763.7 (159.2)	34	2.80	0.008
Extremes	670-1370	510-1100			
<i>Salomonelaps par</i>					
N	22	25			
Mean SVL (\pm SD)	570.6 (44.4)	673.4 (80.5)	45	5.31	0.0001
Extremes	485-640	535-840			
<i>Toxicocalamus loriae</i>					
N	32	37			
Mean SVL (\pm SD)	451.2 (86.7)	501.6 (81.7)	67	2.48	0.016
Extremes	306-650	345-685			

muelleri were recorded in June, November and December. This apparently aseasonal distribution of records suggests that female reproductive cycles in *Aspidomorphus* are either aseasonal, or are asynchronous in different parts of the species range.

Apart from one feather in a specimen of *A. muelleri*, all of the prey items we identified from *Aspidomorphus* were scincid lizards (N = 11 for *A. lineaticollis*, 14 for *A. muelleri*, and 2 for *A. schlegelii*; Table 2). The skins consumed included surface active diurnal heliotherms (e.g., *Car-*

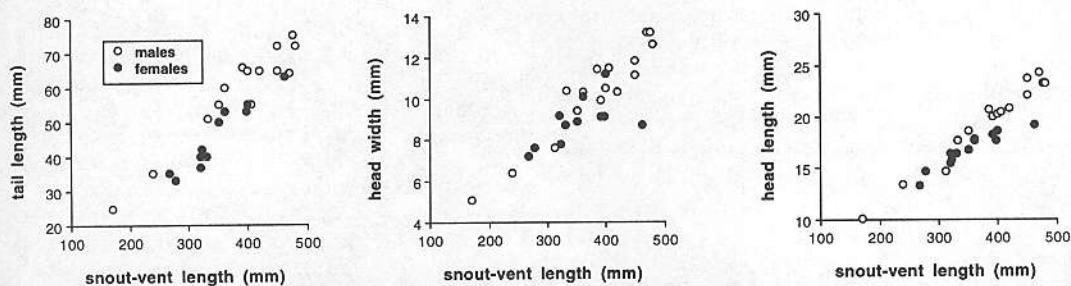


FIG. 1. Sexual dimorphism in body proportions of the New Guinea elapid snake *Aspidomorphus lineaticollis*. At equivalent body lengths, males (circles) have longer tails than do females (dots), and the heads of males are both longer and wider than are those of females. See text for statistical tests of these sex differences.

TABLE 2. Prey items identified from alimentary tracts of Melanesian elapid snakes.

	<i>Aspidomorphus lineaticollis</i>	<i>A. muelleri</i>	<i>A. schlegeli</i>	<i>Looveridgei elapoides</i>	<i>Micropechis ikateka</i>	<i>Salomonelaps par</i>	<i>Toxicocalamus loriae</i>
Earthworms					1	1	13
Frogs							
Lizards							
Gekkonidae							
Scincidae	7	2		1	4	8	
<i>Eugongylus</i> group		3					
<i>Carlia</i> sp.		1	1				
<i>Emoia</i> sp.							
<i>E. cyanura</i>			1				
<i>Sphenomorphus</i> group	4				3	5	
<i>S. jobiensis</i> group					2		
<i>S. pratti</i> group		1					
<i>S. solomonis</i>		1				2	
<i>Tiliqua</i> sp.					1		
Snakes							
Colubridae							
<i>Tropidonophis</i> sp.				1			
Birds							
Mammals		1			2		

lia and *Emoia*) as well as crepuscular semifossorial taxa (e.g., *Sphenomorphus*: Table 2).

(ii) *Loveridgelaps elapoides*.—These large and colorful snakes are crepuscular and nocturnal in habits, and are most often encountered in forested areas adjacent to streams. They spend the daylight hours in leaf litter and under fallen logs (McCoy, 1980 and in litt.). McDowell (1970) recorded a typhlopoid snake in one gut, and a skink in another.

The single mature male that we examined was much smaller than any of the five adult females (Table 1), suggesting that females attain larger body sizes in this taxon. One female (1092 mm SVL) had nine large (23 mm) ovarian follicles. The stomachs of two *Loveridgelaps* contained colubrid snakes, and another *Loveridgelaps* contained scincid scales in its hindgut (Table 2).

(iii) *Micropechis ikaheka*.—This large, heavyset elapid is semifossorial and primarily nocturnal (e.g., Cogger, 1971; Slater, 1956; Parker, 1982; O'Shea, 1991). However, H. G. Cogger (pers. comm.) found one specimen basking in sunlight in the mid-morning, and Hudson (1988) has speculated on possible semiaquatic habits. *Micropechis* is widely distributed across New Guinea, especially in coastal forests (Cogger, 1971). Specific records of dietary items for *Micropechis* include the terrestrial boid *Candoia aspera* (H. G. Cogger, pers. comm.; O'Shea, 1994a), the skink *Sphenomorphus jobiensis*, two scincid tails (McDowell, 1984), the colubrid *Stegonotus* and an unidentified snake (G. Mengden, pers. comm.), the large skink *Tiliqua gigas* (H. G. Cogger, pers. comm.), and a large earthworm (Parker, 1982). O'Shea (1994b) reported cannibalism in captivity.

Males attain much larger body sizes than do females in this species (Table 1). However, the bodily proportions we measured were similar in the two sexes. At the same body lengths, male and female *Micropechis* did not differ in tail length (slopes $F_{1,30} = 0.88$, $P = 0.36$; intercepts $F_{1,31} = 0.11$, $P = 0.74$), head length (slopes $F_{1,30} = 0.10$, $P = 0.76$; intercepts $F_{1,31} = 2.59$, $P = 0.12$) or head width (slopes $F_{1,30} = 4.08$, $P = 0.052$; intercepts $F_{1,31} = 0.79$, $P = 0.38$). Head shape (length relative to width) also did not differ between the two sexes (slopes $F_{1,27} = 0.90$, $P = 0.35$; intercepts $F_{1,28} = 0.004$, $P = 0.98$).

Oviparity was confirmed as the reproductive mode for *M. ikaheka*, based on thick-shelled oviductal eggs, and records of oviposition by freshly-captured females from Karkar Island in October 1965 (H. G. Cogger, pers. comm.). Seven adult female *Micropechis* had clutch sizes of two to seven eggs (mean = 3.86, SD = 1.57). Clutch sizes tended to increase with maternal body size, but this trend fell short of statistical significance ($r = 0.73$, $P = 0.061$). Oviductal eggs ranged in

size from 40 × 29 mm to 65 × 18 mm. Large vitellogenic follicles (>30 mm) were recorded only in August, September and November, oviductal eggs in August, and oviposition in October (see above). Unfortunately, few adult females were collected outside these months, so we cannot infer anything about seasonality of reproduction in this taxon.

We recorded one frog, 10 skinks, two snakes, and two mammals in alimentary tracts of this species (Table 2). In conjunction with the published and other (pers. comm.) records reviewed above, these data suggest that *Micropechis* has a very generalized diet. Although scincid lizards may be the most important prey type, these snakes appear to be willing to consume any terrestrial vertebrate (and perhaps, large invertebrate: Parker, 1982) that they can capture and ingest.

(iv) *Salomonelaps par.*—These medium-sized terrestrial elapids are less fossorial than most of the other endemic Melanesian elapids; they are diurnally active wide-foragers, inspecting crevices for potential prey items as they move through forested areas near streams (McCoy, 1980 and in litt.). McCoy recorded a skink (*Emoia nigra*) and frogs (*Platymantis* and *Ceratobatrachus*) as prey items for *Salomonelaps*. McDowell (1970) listed the following prey records: one with a fish; one with a large beetle; 12 with lygosomine skinks; seven with frogs (*Platymantis* and *Ceratobatrachus*); two with typhlopoid snakes; one with a gecko; and one with the tail of an agamid lizard (probably *Goniocephalus*). Based on their stomach contents and eye sizes, McDowell (1970) inferred that *Salomonelaps* is a surface-active predator that feeds in the litter of the forest floor. He interpreted the high degree of morphological variation within *Salomonelaps* as a reflection of the lack of competition from other, more specialised snake taxa.

Our data show that female *Salomonelaps* grow much larger than conspecific males (Table 1), and have relatively shorter tails (slopes $F_{1,43} = 2.79$, $P = 0.10$; intercepts $F_{1,44} = 28.35$, $P < 0.0001$). However, males and females have similar head sizes at equivalent body lengths (head length: slopes $F_{1,43} = 0.27$, $P = 0.60$; intercepts $F_{1,44} = 3.25$, $P = 0.08$; head width—slopes $F_{1,43} = 2.09$, $P = 0.16$; intercepts $F_{1,44} = 0.70$, $P = 0.41$). Head shape did not differ between the sexes (length relative to width: slopes $F_{1,47} = 1.89$, $P = 0.18$; intercepts $F_{1,48} = 0.19$, $P = 0.67$).

McDowell (1970 and pers. comm.) recorded oviparity in this taxon: a female laid four eggs 29.5 to 35.0 mm long, with parchment-like shells. McDowell (pers. comm.) also recorded clutches of three, four and seven eggs. Clutch sizes of five *S. par* that we examined ranged from three to 12, with an average of 6.4 (SD = 3.65). There was no trend for clutch size to increase with

maternal body size ($r = -0.01$, $P = 0.98$). Adult females with large (>10 mm) ovarian follicles were recorded from November and April.

Our records of prey items for *S. par* include 16 scincid lizards, one frog and one gecko (Table 2). In combination with McDowell's extensive records (see above), we conclude that *Salomonelaps* feeds primarily on lizards (especially skinks) and frogs, but is also prepared to take other vertebrates (and apparently, earthworms) that it encounters.

(v) *Toxicocalamus loriae*.—We noted considerable variation in relative tail length within the *Toxicocalamus* we examined, and hence are unconvinced that our sample represents the single species *T. loriae*. However, most other morphological (and ecological) traits that we measured were relatively conservative, and hence we proceed with the analysis on the assumption that we are dealing with a single taxon. Even if we are in error on this point, it is unlikely to modify our major conclusions.

The snakes of this genus are small and fossorial, and primarily collected from under logs and in leaf litter (Parker, 1982; T. Flannery, pers. comm.). Published dietary records include nine earthworms, one land snail and two fly larva (Bogert and Matalas, 1945; McDowell, 1969), and three earthworms (G. Mengden, pers. comm.). Female *Toxicocalamus* in our sample averaged significantly larger than conspecific males (Table 1), but had shorter tails relative to SVL (slopes $F_{1,17} = 7.36$, $P < 0.015$). Females also had smaller heads than did males of the same body length (head length: slopes $F_{1,17} = 0.12$, $P = 0.73$; intercepts $F_{1,18} = 17.94$, $P < 0.0005$; head width—slopes $F_{1,17} = 0.30$, $P = 0.59$, intercepts $F_{1,18} = 5.42$, $P < 0.032$). Head shape (length relative to width) did not differ between the sexes (slopes $F_{1,19} = 0.13$, $P = 0.72$; intercepts $F_{1,20} = 0.01$, $P = 0.94$).

Thick-shelled oviductal eggs (28 to 35 mm long) in our dissected specimens confirmed McDowell's (1969) report of oviparity as the reproductive mode for *Toxicocalamus*. Clutch sizes of 15 *Toxicocalamus* ranged from one to eight, with a mean of 5.53 (SD = 1.81). Larger females produced larger clutches ($r = 0.64$, $P < 0.011$). Females with enlarged (>15 mm) ovarian follicles were recorded in February through May. All 13 prey items that we recorded were earthworms (Table 2), suggesting that *Toxicocalamus* feed primarily (perhaps exclusively, if three earlier records are in error) on earthworms. Unlike all of the other Melanesian and Australian elapids, *Toxicocalamus* apparently does not prey upon vertebrates.

DISCUSSION

The primary aims of our study were to document some aspects of the basic biology of the

endemic Melanesian elapids, and to compare these tropical snakes with temperate zone elapids in Australia. The comparison with Asian elapids is also of interest, since the phylogenetic affinities of the Melanesian taxa may lie with Asia as well as with Australia. However, the comparison with the Australian elapids is the strongest, because the Asian fauna is less speciose, is entirely tropical, and is poorly-known in comparison to the Australian elapids. Not surprisingly, our data reveal many points of similarity between the endemic Melanesian elapids and their relatives in other countries. Nonetheless, there appear to be at least two significant differences (i.e., distinctive features of the Melanesian fauna) as well.

(i) *Diets*.—It is possible to identify ecological analogues of some of the Melanesian elapids among the elapids of Asia and Australia. Thus, for example, *Aspidomorphus* is highly convergent with Australian elapids of the genera *Cacophis* and *Furina* in its morphology, coloration, nocturnal behavior, and specialization on scincid lizards (Shine, 1980a, 1981). Similarly, the medium-sized *Salomonelaps* is a generalised diurnal forager that feeds primarily on lizards and frogs, like many similarly-sized elapids from Australia (e.g., *Hemiaspis*, *Pseudechis*: Shine, 1994a). The apparent specialization of *Loveridgelaps* on reptilian prey (especially snakes?) mirrors the situation in other semifossorial elapids such as the Australian *Vermicella* (Shine, 1980b), and the Asian *Bungarus*, *Calliophis*, and *Maticora* (Werler and Keegan, 1963; Leviton, 1964). *Micropechis* has a generalized diet, like that of many large elapids from other countries (e.g., *Austrelaps*—Shine, 1994a; *Naja*—Werler and Keegan, 1963). However, the microhabitats used by *Loveridgelaps* and *Micropechis* (especially their apparent reliance on leaf litter), and hence their foraging behavior, may be rather different from that of the more surface-active large elapids from Asia and Australia. Presumably, the importance of leaf litter habitats to the Melanesian snakes reflects the abundance of these habitats in Melanesia relative to other Old World areas where elapids are found.

By far the most distinctive taxon, in terms of diet, is *Toxicocalamus*. The specialization of this group on invertebrates (earthworms and soft-bodied insects) is shared by only one other Old World elapid: the endemic Fijian bola, *Ogmodon vitiensis* (Zug and Ineich, 1993). This dietary similarity thus reinforces the suggestion of a close phylogenetic affinity between *Ogmodon* and *Toxicocalamus* (Bogert and Matalas, 1945; McDowell, 1967, 1969). There are no invertebrate specialists among the diverse array of Australian elapids, even among the many small fossorial taxa that superficially resemble *Toxicocalamus* (Shine, 1994a). The Asian elapid fauna

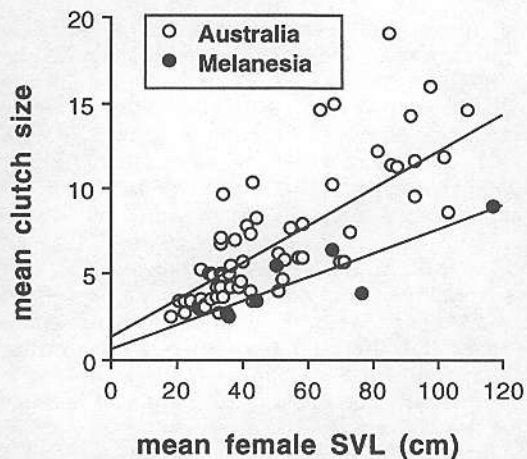


FIG. 2. An interspecific comparison of mean clutch sizes relative to maternal body sizes (snout-vent length, = SVL) in Australian elapid snakes (circles) and Melanesian elapid snakes (dots). Relative to maternal body size, Melanesian species have smaller clutches. See text for statistical tests. Data for Australian snakes from Shine (1994a).

also contains fossorial species (*Bungarus*, *Calliophis*, *Maticora*), but all feed primarily on other snakes, not on invertebrates (Werler and Keegan, 1963; Leviton, 1964; Slowinski, 1994). As far as we are aware, the only other invertebrate specialists among the elapids are some species of South American coral snakes of the genus *Micrurus* (e.g., Dixon and Soini, 1986). Hence, invertebrate-eating among the elapids appears to be restricted to tropical species, whereas this is certainly not the case in either colubrids or viperids (see below).

Why do *Toxicocalamus* and *Ogmodon* feed on soft-bodied invertebrates, unlike any other congeneric taxa in Asia or Australia? Invertebrate-eating habits are the rule in scolecophidian snakes (e.g., *Ramphotyphlops*—Webb and Shine, 1993), and invertebrates are also eaten by diverse lineages of colubrids (e.g., *Chionactis*, *Coluber*—Wright and Wright, 1957) and viperids (e.g., *Echis*, *Vipera ursinii*—Duff-Mackay, 1965; Baron, 1990) from a diverse array of habitats, including deserts. We have no answer as to why such a diet is rare in elapids, and restricted to tropical taxa within this group. The prevalence of earthworms in the diet of *Toxicocalamus*, compared to predation on vertebrates by superficially similar Australian taxa, has interesting analogies in at least two other lineages. In both typhlopids and monotremes (echidnas), a New Guinea species eats earthworms while its Australian relatives eat ants (Augee, 1992; Webb and Shine, 1993). These parallels may reflect the greater abundance of earthworms in

the deep fertile soils and high rainfall areas of New Guinea, than in the relatively impoverished soils and dry climates over most of mainland Australia (Flannery, 1994).

(ii) *Reproduction*.—Are there distinctive features of the reproductive biology of the Melanesian elapids? Oviparity is widespread (perhaps ubiquitous) in the Melanesian elapids, but is also the most common reproductive mode in the elapids of northern Australia (see map in Shine, 1991a, pp. 109). Although some of the Melanesian elapids may breed over an extended season, our results are equivocal in this respect and many northern Australian elapids may have similarly long durations of reproductive activity (Shine, 1991a). In terms of reproductive output, however, the Melanesian elapids are distinctive. All of the species we examined have clutch sizes that are lower than those of most comparably-sized Australian elapid species. This result is clearly evident from Fig. 2, which shows that the Melanesian species fall below the average size-specific clutch for confamilial Australian species. Analysis of covariance (with region as the factor, and maternal body length as the covariate) confirms that this difference is greater than would be expected by chance (slopes $F_{1,74} = 1.26$, $P = 0.27$; intercepts $F_{1,75} = 10.97$, $P < 0.0015$). This result mirrors that of other workers who have documented a reduction in size-specific fecundity in tropical reptiles, compared to confamilial species from more seasonal habitats. The reduced clutch size translates into a lower relative clutch mass (RCM) in some of these taxa, but is opposed by a compensating increase in offspring size in others (Barbault, 1975; Rand, 1982; James and Shine, 1988; Forsman and Shine, 1996). We suspect that RCMs may be lower in the Melanesian elapids than in the Australian species, based on our observation that the gonads (and, in gravid females, the eggs) occupy a relatively small proportion of maternal body length. Data on RCMs and offspring sizes for these snakes would be of great interest, and help to clarify the issue of whether the low fecundity of the Melanesian elapids reflects lower total investment per clutch (perhaps related to a higher reproductive frequency?) or simply a change in the packaging of the clutch (into fewer, larger offspring).

Are clutch sizes consistently lower in tropical snakes than in temperate zone species overall? Available data are insufficient for rigorous analysis, but the pattern seems to be strong. Aldridge et al. (1995) documented a significant intraspecific difference in size specific fecundity between tropical versus temperate populations of a natricine watersnake, and Dunham et al.'s (1988) analysis of published data detected a significant difference in fecundity relative

to maternal body size in tropical versus temperate-zone snakes. Although a similar review led Aldridge et al. (1995) to conclude that tropical species did not differ from temperate species in this respect, their data reveal a major difference in mean clutch sizes (6.0 versus 18.3), and an almost-significant difference in size-specific fecundities (using log-transformed values for both variables: ANCOVA slopes $F_{1,28} = 0.58$, $P = 0.45$; slopes $F_{1,29} = 3.89$, $P = 0.058$). Thus, the apparent tropical-temperate fecundity differences in snakes warrant further study.

The paucity of information on behavior of Melanesian elapids in the wild or in captivity makes it difficult to interpret other aspects of their biology. For example, one obvious dichotomy in our data is between those species in which males grow much larger than females (*Micropechis* and *Aspidomorphus*), versus those in which the female is the larger sex (*Loveridgelaps*, *Salomonelaps*, *Toxicocalamus*). Comparative analyses on other snake species suggest that larger male than female size usually occurs in species that display male-male combat during the breeding season (Shine, 1994b). Hence, we predict that mating systems may differ between the two groups listed above, with male-male combat restricted to the former two genera, but we have no information with which to test this prediction. Other aspects of sexual dimorphism remain equally elusive. Relatively longer tails in males than in females have been previously reported for *Toxicocalamus* (Bogert and Matalas, 1945) and this phenomenon is widespread among snakes in general, probably for several reasons (King, 1989). Sexual dimorphism in relative head length (as we documented in *Aspidomorphus* and *Toxicocalamus*) is also relatively common in snakes, and may be related to sex-specific divergence in diets (Shine, 1991b). Interestingly, although males have relatively larger heads than same-sized females in both of these groups, the direction of body-size dimorphism is different (males larger in *Aspidomorphus*, females larger in *Toxicocalamus*). Thus, the effect of the relatively larger head size in males is to amplify the sex difference in mean head lengths in *Aspidomorphus* but to decrease it in *Toxicocalamus*. Unfortunately, data on the diet of these snakes (Table 2) are too fragmentary to provide any useful test of the hypothesis that this divergence is related to divergences in the sizes of prey items consumed by the two sexes.

Lastly, we emphasise the ecological diversity that our study reveals among the endemic Melanesian elapids. The five genera we examined varied considerably in absolute size, in the direction and degree of sexual dimorphism in body size and in relative head size, in diets and in

reproductive output. Our analysis certainly underestimates the ecological diversity among this group, because we were unable to examine representatives of several species that have been inferred to display unique trophic relationships, based on the morphology of their feeding structures (e.g., *Parapistocalamus*, and some taxa within *Toxicocalamus*—McDowell, 1969). Information on these taxa, and more detailed data on the behavior and ecology of all of the Melanesian elapid species, will be needed before we can obtain a clear picture of the overall biology of these tropical snakes. If we are to interpret the functional (adaptive) significance of the traits concerned, we will also need a reliable phylogenetic hypothesis for the group (Harvey and Pagel, 1991). Our study suggests that tropical snakes may indeed have distinctive ecological characteristics, but it also throws into sharp relief the extent of our ignorance about even the most abundant tropical species.

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LITERATURE CITED

- ALDRIDGE, R. D., W. P. FLANAGAN, AND J. T. SWARTHOUT. 1995. Reproductive biology of the water snake *Nerodia rhombifer* from Veracruz, Mexico, with comparisons of tropical and temperate snakes. *Herpetologica* 51:182-192.
- AUGEE, M. L. 1992. Platypus and Echidnas. Royal Zoological Society of New South Wales, Sydney.
- BARBAULT, R. 1975. Observations ecologiques sur la reproduction des lézards tropicaux: Les stratégies de ponte en forêt et en savane. *Bull. de la Soc. Zool. de France* 100:153-167.
- BARON, J. P. 1990. Régime et cycles alimentaires de la vipère d'orsini (*Vipera ursinii* Bonaparte, 1835) au Mont Ventoux (France). Doctoral Thesis, Ecole Pratique des Hautes Etudes, Paris.
- BOGERT, C. M., AND B. L. MATALAS. 1945. Results of the Archbold Expeditions. No. 53. A review of the elapid genus *Utrococalamus* of New Guinea. *Amer. Mus. Novit.* 1284:1-8.
- BRANCH, W. R. 1988. A Field Guide to the Snakes and Other Reptiles of Southern Africa. Struik, Cape Town.
- COGGER, H. G. 1971. The venomous snakes of Australia and Melanesia. In W. Bucherl and E. E. Buckley (eds.), *Venomous Animals and Their Venoms*, Vol. 2, pp. 35-77. Academic Press, New York.

- DIXON, J. R., AND P. SOINI. 1986. The Reptiles of the Upper Amazon Basin, Iquitos Region, Peru. Milwaukee Public Museum, Milwaukee.
- DUFF-MACKAY, A. 1965. Notes on the biology of the carpet viper, *Echis carinatus pyramidum* (Geoffroy), in the northern frontier province of Kenya. J. E. A. Nat. Hist. Soc. 25:28-40.
- DUNHAM, A. E., D. B. MILES, AND D. N. REZNICK. 1988. Life history patterns in squamate reptiles. In C. Gans and R. B. Huey (eds.), *Biology of the Reptilia*, Vol. 16, pp. 441-522. A. R. Liss, New York.
- DUNSON, W. A., AND S. A. MINTON. 1978. Diversity, distribution, and ecology of Philippine marine snakes (Reptilia, Serpentes). J. Herpetol. 12:281-286.
- FITCH, H. S. 1982. Reproductive cycles in tropical reptiles. Occ. Pap. Mus. Nat. Hist. Univ. Kansas 96:1-53.
- FLANNERY, T. F. 1994. *The Future Eaters*. Reed Books, Sydney.
- FORSMAN, A., AND R. SHINE. 1996. Parallel geographic variation in body shape and reproductive life history within the Australian scincid lizard *Lampropholis delicata*. *Funct. Ecol.* 9:818-828.
- GREENE, H. W. 1984. Feeding behavior and diet of the eastern coral snake, *Micrurus fulvius*. In R. A. Seigel, L. E. Hunt, J. L. Knight, L. Malaret and N. L. Zuchslag (eds.), *Vertebrate Ecology and Systematics—Tribute to Henry S. Fitch*, pp. 147-162. Museum of Natural History, Univ. Kansas, Lawrence.
- HARVEY, P. H., AND M. D. PAGEL. 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- HUDSON, B. J. 1988. The small-eyed snake (*Micropechis ikaheka*): a review of current knowledge. *Papua New Guinea Med. J.* 31:173-178.
- JACKSON, D. R., AND R. FRANZ. 1981. Ecology of the eastern coral snake (*Micrurus fulvius fulvius*) in northern peninsular Florida. *Herpetologica* 37:213-228.
- JAMES, C. D., AND R. SHINE. 1988. Life-history strategies of Australian lizards: a comparison between the tropics and the temperate zone. *Oecologia* (Berlin) 75:307-316.
- KING, R. B. 1989. Sexual dimorphism in snake tail length: sexual selection, natural selection, or morphological constraint? *Biol. J. Linn. Soc.* 38:133-154.
- LEVITON, A. E. 1964. Contributions to a review of Philippine snakes, III. The genera *Maticora* and *Calliophis*. *Philippine J. Sci.* 92:523-550.
- MCCOY, M. 1980. *Reptiles of the Solomon Islands*. Wau Ecology Institute, Handbook No. 7, Honolulu.
- MCDOWELL, S. B. 1967. *Aspidomorphus*, a genus of New Guinea snakes of the family Elapidae, with notes on related genera. *J. Zool. (London)* 151:497-543.
- . 1969. *Toxicocalamus*, a New Guinean genus of snakes of the family Elapidae. *J. Zool. (London)* 159:443-511.
- . 1970. On the status and relationships of the Solomon Island elapid snakes. *J. Zool. (London)* 161:145-190.
- . 1984. Results of the Archbold Expeditions. No. 112. The snakes of the Huon Peninsula, Papua New Guinea. *Amer. Mus. Novit.* 2775:1-28.
- O'SHEA, M. 1991. The reptiles of Papua New Guinea. *Brit. Herp. Soc. Bull.* 37:15-32.
- . 1994a. *Micropechis ikaheka* (small-eyed or Ikaheka snake). *Ophiophagy. Herpetol. Rev.* 25:70.
- . 1994b. *Micropechis ikaheka* (small-eyed or Ikaheka snake). *Cannibalism. Herpetol. Rev.* 25:70-71.
- PARKER, F. 1982. *The Snakes of Western Province*. Division of Wildlife, Konedobu.
- PARKER, W. S., AND M. V. PLUMMER. 1987. Population ecology. In R. A. Seigel, J. T. Collins and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 253-301. Macmillan, New York.
- PERNETTA, J. C. 1977. Observations on the habits and morphology of the sea snake *Laticauda colubrina* (Schneider) in Fiji. *Can. J. Zool.* 55:1612-1619.
- RADCLIFFE, C. W., AND D. A. CHISZAR. 1980. A descriptive analysis of predatory behavior in the yellow lipped sea krait (*Laticauda colubrina*). *J. Herpetol.* 14:422-424.
- RAND, A. S. 1982. Clutch and egg size in Brazilian iguanid lizards. *Herpetologica* 38:171-178.
- SHINE, R. 1980a. Comparative ecology of three Australian snake species of the genus *Cacophis* (Serpentes: Elapidae). *Copeia* 1980:831-838.
- . 1980b. Reproduction, feeding and growth in the Australian burrowing snake *Vermicella annulata*. *J. Herpetol.* 14:71-77.
- . 1981. Ecology of the Australian elapid snakes of the genera *Furina* and *Glyphodon*. *J. Herpetol.* 15:219-224.
- . 1991a. *Australian Snakes. A Natural History*. A. H. and A. W. Reed, Sydney.
- . 1991b. Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *Amer. Natur.* 138:103-122.
- . 1994a. Allometric patterns in the ecology of Australian snakes. *Copeia* 1994:851-867.
- . 1994b. Sexual size dimorphism in snakes revisited. *Copeia* 1994:326-346.
- , AND L. SCHWARZKOPF. 1992. The evolution of reproductive effort in lizards and snakes. *Evolution* 46:62-75.
- SLATER, K. R. 1956. *A Guide to the Dangerous Snakes of Papua*. Govt. Publisher, Port Moresby.
- SLOWINSKI, J. B. 1994. The diet of kraits (Elapidae: *Bungarus*). *Herpetol. Rev.* 25:51-53.
- TINKLE, D. W. 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. *Amer. Natur.* 103:501-516.
- , H. M. WILBUR, AND S. G. TILLEY. 1970. Evolutionary strategies in lizard reproduction. *Evolution* 24:55-74.
- VITT, L. J. 1987. Communities. In R. A. Seigel, J. T. Collins and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 335-365. Macmillan, New York.
- VORIS, H. K., AND B. C. JAYNE. 1979. Growth, reproduction and population structure of a marine snake, *Enhydrina schistosa* (Hydrophiidae). *Copeia* 1979:307-318.
- , H. H. VORIS, AND L. BOO-LIAT. 1978. The food and feeding behaviour of a marine snake, *Enhydrina schistosa* (Hydrophiidae). *Copeia* 1978:131-146.
- WEBB, J. K., AND R. SHINE. 1993. Dietary habits of Australian blindsnakes. *Copeia* 1993:762-770.

- WERLER, J. E., AND H. L. KEEGAN. 1963. Venomous snakes of the Pacific area. In H. L. Keegan and W. V. Macfarlane (eds.), *Venomous and Poisonous Animals and Noxious Plants of the Pacific Region*, pp. 219-325. Macmillan Co., New York.
- WRIGHT, A. H., AND A. A. WRIGHT. 1957. *Handbook of Snakes of the United States and Canada*. Cornell Univ. Press, Ithaca.
- ZUG, G. R., AND I. INEICH. 1993. Review of the biology and morphology of the Fijian bola, *Ogmodon vitianus* (Elapidae). *The Snake* 25:9-20.

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