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Relationships between sexual dimorphism and niche partitioning within a clade of sea-snakes (Laticaudinae)

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Abstract Previous studies in Fiji have shown that females of the amphibious sea-krait *Laticauda colubrina* are much larger than males, and have larger heads relative to body size. The dimorphism has been interpreted in terms of adaptation to a sex divergence in prey-size: females primarily eat large (conger) eels rather than smaller (moray) eels. The hypothesis that dimorphism is affected by niche divergence predicts that the degree of sex dimorphism will shift when such a species invades a habitat with a different range of potential prey sizes. On the island of Efate in Vanuatu, *L. colubrina* and a regionally endemic sibling species (*L. frontalis*) both consume smaller eels (in absolute terms, and relative to the snake's body size) than do the previously-studied Fijian snakes. Patterns of morphology and sexual dimorphism have shifted also. Both Vanuatu taxa are slender-bodied, and *frontalis* is smaller and less dimorphic than *L. colubrina*. Females grow larger than males in all taxa, and have larger heads (relative to body length), but the degree of sexual divergence is lower in Vanuatu (especially in *frontalis*). Dietary overlap (in prey species as well as size) is high between adult *frontalis* and juvenile *colubrina*, but the two taxa differ in prey size/predator size relationships. In particular, male *frontalis* eat very small prey and have very short heads. Our results are consistent with the hypothesis that sex differences in the mean adult body sizes and relative head sizes of laticaudine snakes are linked to sex differences in feeding biology.

Keywords · Diet · Niche · *Laticauda colubrina* · *Laticauda frontalis* · Vanuatu

Introduction

“Jack Sprat could eat no fat, His wife could eat no lean, So between them both, you see, they licked the platter clean” – Old English nursery rhyme.

In many animal species, males and females differ considerably in mean adult body sizes and shapes. Sexual dimorphism of this kind has generally been attributed to the action of sexual selection and fecundity selection (e.g. Andersson 1994), but ecological (niche) divergence offers an alternative explanation for the evolution of sex differences in morphology (e.g. Selander 1966; Shine 1989; Temeles et al. 2000). For example, males and females might evolve to be of different adult body sizes because they feed on different-sized prey. Mathematical models confirm the plausibility of this hypothesis. If underlying resource distributions generate bimodal adaptive peaks for body size, then the two sexes might evolve so as to occupy these different “optimal body sizes” (Slatkin 1984).

Although this is a simple idea, it is difficult to test. There are many species in which the sexes differ not only in size and/or shape, but also in niche dimensions such as prey size (e.g. Shine 1989; Andersson 1994). Nonetheless, such sex divergences might be consequences of (rather than selective forces for) evolutionary shifts in sexual dimorphism. A more powerful approach would be to examine patterns of sexual dimorphism and resource use within a clade of closely-related taxa in habitats with different prey-size distributions. Under such circumstances, the “ecological causation” hypothesis would predict shifts in patterns of sexual dimorphism in body size or trophic (feeding) structures. The best system for testing this prediction would involve species in which a predator's body size affects its maximal prey size (e.g. through gape-limitation) and where adaptations to feeding on prey of different sizes are readily detected in morphology of the feeding structures (e.g. relative head size or shape). Snakes fulfill these conditions, and hence provide some of the best examples of sexual dimorphism related to niche divergence (Shine 1991). For example,

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three distantly-related species of aquatic snakes all have females much larger than males, with relatively larger heads, and eating much larger prey items (acrochordids – Houston and Shine 1993; natricine colubrids – Mushinsky et al. 1982; laticaudids – Shetty and Shine 2001).

Between 1983 and 1996 extensive field and laboratory research on laticaudine sea kraits was conducted in the western Pacific under the leadership of Professor Nobuo Tamiya (Tohoku University) and Dr. Toru Tamiya (Sophia University). One outcome of this research was the discovery that populations of the yellow-lipped sea krait (*Laticauda colubrina*) in Vanuatu actually comprised two syntopic sibling species – the larger *Laticauda colubrina* (s.s.) and a much smaller sister species, for which the name *Laticauda frontalis* (DeVis 1905) is available (Cogger et al. 1987). We have now used this system to examine correlated shifts in dietary habits and sexual dimorphism between two areas with different prey-size spectra.

Materials and methods

Study area

Vanuatu is a nation comprising approximately 80 islands in the Pacific Ocean, 170 km south of the Solomon Islands, 800 km west of Fiji and 230 km north-east of New Caledonia. The climate is warm year-round, with mean minima/maxima of 19/27°C in July and 24/30°C in January. Rainfall is concentrated in the period from December to February (O'Byrne and Harcombe 1999). We worked on the island of Efate, within 20 km of the village of Paoningisu (Nagar Resort: 17°35'S, 168°29'E).

Study species

The laticaudine sea-snakes ("sea kraits") comprise a lineage of proteroglyphous venomous snakes that may be most closely related to either the Australian or Asian terrestrial elapids (Slowinski 1989; Keogh et al. 1998). They invaded marine habitats independently of the other major group of sea-snakes, the Hydrophiidae (Heatwole 1999). Laticaudines forage in the ocean, but return to land to mate, lay eggs, digest their prey, and shed their skins. Three laticaudine sea-snake taxa occur in Vanuatu, all belonging to a clade of species that feed primarily or exclusively on eels (Cogger et al. 1987; Greer 1997). One species, *L. laticaudata*, is an elongate snake with blue markings between its black bands: it is morphologically distinctive from the other two taxa and will not be considered further in the present paper.

The other two sea krait species in Vanuatu are so similar to each other in external morphology that they have generally been treated as conspecific, even in detailed taxonomic revisions (e.g. McCarthy 1986; Greer 1997). They are more heavy-bodied than *L. laticaudata*, and have white-and-black rather than blue-and-black bands. Recent morphological studies have resurrected *frontalis* from synonymy with *colubrina*: the two taxa differ from each other in body sizes and midbody scale-rows and other scale counts and (less consistently) in minor aspects of color pattern (Cogger et al., unpublished data). Examination of large series of specimens from Efate has revealed no instances of hybridization (H.G. Cogger, personal communication). Species isolation is maintained by species-specific male courtship, based in turn upon differences in pheromone profiles between females of the two species (Shine et al. 2002).

The larger species (*L. colubrina*) is widespread from Fiji in the east through to the Andaman Islands in the west. Average adult body size appears to be conservative over this wide geographic range, up to approximately 150 cm snout-vent length (SVL) and

1,800 g in females versus 100 cm SVL and 600 g in males (McCarthy 1986; Cogger et al. 1987; Shetty and Prasad 1996; Heatwole 1999; Shetty 2000). At least in Fijian *L. colubrina* (the only laticaudine population for which we have detailed data), this sexual size dimorphism is associated with niche partitioning between the sexes. Adult males, and juveniles of both sexes, feed on small shallow-water eel species, mostly morays. In contrast, adult female sea kraits take large deep-water eels, mainly congers (Shetty 2000; Shetty and Shine 2001). In keeping with this dietary divergence, the heads of female *L. colubrina* in Fiji are larger than are those of males at the same SVL (Camilleri and Shine 1990; Shetty 2000; Shetty and Shine 2001).

Methods

We visited Efate from October to December 2000. Snakes were captured by hand, either from crevices in rocks or mangrove trees during the day, or as the snakes swam or crawled around near the shoreline at night. The animals were held in cloth bags or outdoor arenas until processing (generally <24 h after capture). Prey items were detected by palpation and removed by forced regurgitation. Most prey were partially digested, but (because all were eels, so that body shape was consistent over most of the animal's length), we could reliably measure maximal diameter of the prey item. This is the most crucial dimension in terms of gape-limitation for a predatory snake (Greene 1983). All eels were identified with available taxonomic keys, and also photographed for later comparison with preserved specimens in the collection of the Australian Museum. Each snake was measured (SVL and tail length), weighed, and individually marked by scale-clipping. Sex was determined by tail shape (Shine and Shetty 2001). We also counted the number of midbody scale-rows. Processed snakes were either retained for behavioral studies, or released the next day. All remaining snakes were released at the conclusion of the study.

We did not dissect any snakes, so do not have morphological criteria for the body size at sexual maturation in either taxon. However, extensive dissections of Fijian *L. colubrina* (with a very similar body-size distribution to our Vanuatu samples) showed that males mature at 70 cm SVL and females at 90 cm SVL (Guinea 1986; Shetty 2000). There have been no previous ecological studies on *L. frontalis*. We estimated a body size at maturation of 40 cm SVL for male *frontalis* and 50 cm SVL for females; low numbers of animals on either side of this cut-off mean that, even if we are in error, this should have little effect on our estimates of mean adult body size or sexual size dimorphism (see below).

Predictions and shortcomings

If sexual dimorphism in adult body sizes and trophic structures (relative head size, head shape) is influenced by adaptation to sex-specific niches, we would predict that geographic variation in prey resources (especially, prey sizes) would be reflected in concurrent geographic variation in sexual dimorphism. An alternative interpretation for the correlation between dimorphism and niche divergence within Fijian sea kraits is that the sex divergence in diets arose as a consequence of the sexual dimorphism rather than acting as a selective force on dimorphic traits. Under this latter hypothesis, we might expect to see that the direction and degree of sexual dimorphism remained relatively conservative within the laticaudid clade, even if prey sizes differed appreciably among areas. Additionally, we might expect that there would be weaker (if any) relationships between sexual dimorphism and niche divergence. Thus, we set out to describe patterns of sexual dimorphism in the Vanuatu laticaudids, and to compare prey types and sizes consumed by males and females of each species. Our study was hampered by two main methodological shortcomings:

1. Because phylogenetic relationships among the study taxa are unknown, we cannot discern the direction of change in attributes of morphology and ecology within this clade.

2. Because of the difficulty of quantifying prey availability for highly mobile predators, we cannot quantify the availability of eels of different sizes in Vanuatu versus Fiji. We have seen many more large eels in Fiji than in Vanuatu during snorkel and scuba dives in the two areas (>30 versus 0; see also Myers 1989; Randall et al. 1997; Michael 1998; Bohlke and Randall 2000), but it is difficult to translate these observations into measures (or even indices) of the availability of prey of different sizes. For example, a particular eel species might be abundant and obvious to human observers, but essentially inaccessible to the snakes because it uses refuges impenetrable to snakes, or has behaviors that facilitate escape. Thus, although limited observations suggest that sea-snakes in Fiji have access to more large prey items than do those in Vanuatu, ultimately the most reliable data on this topic will come from the gut contents of captured snakes rather than estimates from visual censuses on reefs.

Analysis

Linear measures were ln-transformed prior to analysis, to meet the assumption of normality of distributions for parametric tests. We compared these traits between sexes and among species and locations using ANOVA and ANCOVA. Categorical variables (such as numbers of different prey taxa) were compared between species and sexes using contingency-table analyses. To compare our results to those of previous studies on Fijian *colubrina*, we used raw data from Shetty's (2000) work. We can thus compare *colubrina* in an apparently resource-poor area to (1) the same species in an area with a broad resource base, and (2) a species (*frontalis*) that has evolved in this apparently resource-poor area. For analysis, we used Statview 5 and SuperAnova 1.1 on a Macintosh G4 computer. The data sets for all analyses, except overall sexual size dimorphism (SSD), omitted snakes ≥ 90 cm SVL, to ensure sufficient overlap between the taxa. We also analyzed data from snakes <70 cm SVL (to ensure complete overlap among all groups), but these generated results virtually identical to those for snakes <90 cm SVL, and thus are not reported.

Results

We first consider the data from Vanuatu only.

Sample sizes

During our fieldwork in Vanuatu, we collected 211 *L. colubrina* and 39 *L. frontalis* (Table 1). Although the rel-

ative numbers of each species (and of juveniles and adults within each species) varied among the four localities that we sampled, contingency-table analysis revealed no significant departure from the null expectation of random distribution of each group among sites ($\chi^2=15.82$, $df=15$, $P=0.39$).

Body sizes and sexual size dimorphism

Females attained larger body sizes than males in both species, but the size disparity between the sexes was much greater in *colubrina* than in *frontalis* (Fig. 1, Table 1). A two-factor ANOVA on the body sizes (ln SVLs) of adult animals confirms that the degree of SSD was much greater in *colubrina* than in *frontalis* (interaction $F_{1,135}=56.60$, $P=0.0001$). Using the index of SSD proposed by Lovich and Gibbons (1992), *colubrina* has a score of 0.496 (females averaged 50% longer than males) whereas *frontalis* averages 0.170 (females were 17% longer). On average, adult female *colubrina* weighed >3 times as much as conspecific males, whereas adult female *frontalis* weighed one-third more than adult male *frontalis*.

Body shape

The two species followed similar regression lines for mass versus snout-vent length (Fig. 2). ANCOVA with sex and species as factors, and ln mass as the dependent variable, nonetheless showed statistically significant differences in mass relative to SVL. Slopes were homogeneous (all interaction P values >0.12) and the same was true for all ANCOVA results below, unless interaction terms are shown. Intercepts for ln mass relative to ln SVL differed between sexes ($F_{1,225}=17.81$, $P<0.0001$) and species ($F_{1,225}=28.00$, $P<0.0001$). Inspection of residual scores (from the linear regression of ln mass versus ln SVL) shows that males were more heavy-bodied than females of the same SVL, and *frontalis* were more heavy-bodied than *colubrina* (Fig. 3a).

Table 1 Sample sizes, mean adult body sizes and sexual size dimorphism in Vanuatu specimens of the sympatric sea-krait species *Laticauda colubrina* and *L. frontalis*. Entries in Table show mean values, with standard deviations in parentheses

	<i>L. colubrina</i>			<i>L. frontalis</i>		
	Juveniles	Males	Females	Juveniles	Males	Females
Sample size in each locality:						
Main island of Efate	34	30	23	11	5	4
Offshore islands	23	12	7	3	2	1
Mangrove clump	15	8	6	0	0	0
Kakula Island	23	17	13	3	7	3
Snout-vent length (cm)	57.97 (12.66)	78.25 (4.88)	117.05 (15.11)	37.80 (5.30)	57.44 (3.94)	67.61 (7.99)
Tail length (cm)	7.02 (1.76)	11.96 (1.09)	12.05 (1.47)	4.80 (0.89)	7.98 (0.75)	6.91 (0.86)
Head length (mm)	18.57 (3.44)	22.77 (1.72)	35.50 (4.93)	13.54 (1.31)	17.39 (1.24)	20.21 (2.45)
Head width (mm)	10.81 (2.13)	13.28 (1.08)	23.81 (5.06)	7.32 (0.55)	10.23 (0.84)	11.11 (1.30)
Number of midbody scale rows	24.07 (1.13)	23.26 (0.62)	25.05 (0.51)	21.00 (0.00)	21.05 (0.22)	21.18 (0.60)
Total number of bands	36.97 (1.98)	37.34 (1.59)	36.98 (1.92)	36.40 (3.21)	36.38 (1.84)	38.18 (2.40)

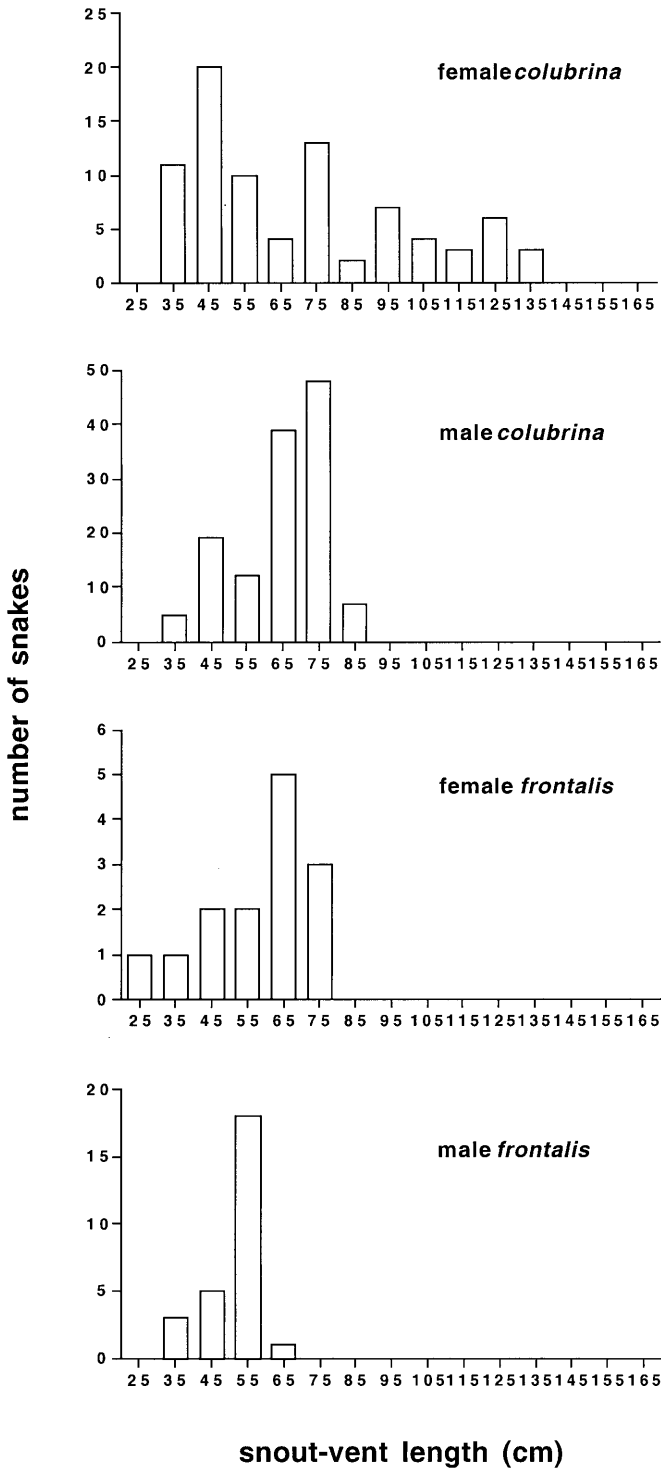


Fig. 1 Frequency distributions of body sizes (snout-vent lengths) for male and female specimens of the sea-snakes *Laticauda colubrina* and *L. frontalis*, collected on or near the island of Efate in Vanuatu

Relative head length

ANCOVA also revealed sex and species differences in head length relative to SVL. At the same body length, females had longer heads than did males (main effect of

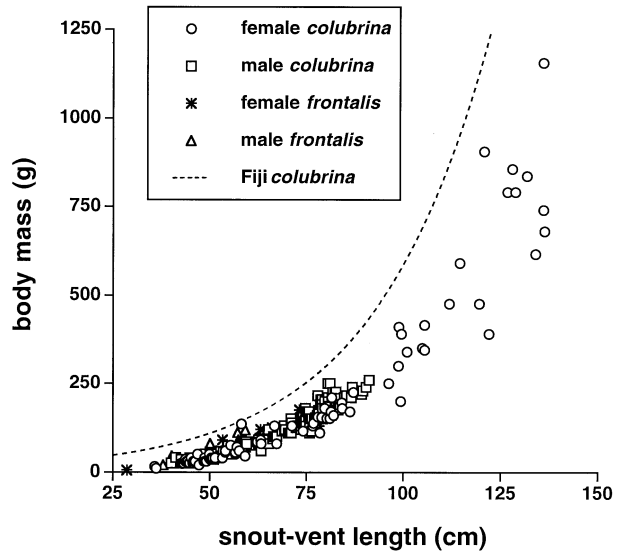


Fig. 2 Mass relative to snout-vent length for male and female specimens of the sea-snakes *Laticauda colubrina* and *L. frontalis*. The dotted line shows calculated line of best fit to data from Fijian specimens of *L. colubrina*, from Shetty (2000)

sex $F_{1,219}=36.30$, $P=0.0001$), and relative head sizes were larger in *colubrina* than in *frontalis* (main effect of species $F_{1,219}=12.34$, $P=0.0005$; see Fig. 3b). However, Fig. 3b also reveals an interaction in this respect: the degree of sexual dimorphism in relative head length was greater in *colubrina* than in *frontalis* (interaction $F_{1,243}=6.42$, $P=0.012$).

Relative head width

ANCOVA of ln head width on ln SVL generated a significant three-way interaction term among SVL, sex and species ($F_{1,220}=5.32$, $P=0.02$). To clarify this result, we calculated an index of head shape (residual scores from the linear regression of ln head width versus ln head length). A two-factor ANOVA on this variable generated a significant two-way interaction term ($F_{1,218}=4.64$, $P=0.03$): head shape was similar overall in the two species, but the degree of sexual dimorphism in this trait differed between the two taxa (Fig. 3c). Male and female *colubrina* had similar-shaped heads, but male *frontalis* had relatively wider heads than did females of the same species.

Number of dorsal scale-rows

The number of dorsal scale rows at midbody varied as a function of the snake's sex and species (interaction $F_{1,216}=51.71$, $P<0.0001$). Female *colubrina* usually had 25 scale rows, whereas males had 23. In contrast, both sexes of *frontalis* usually had 21 scale rows (Table 1).

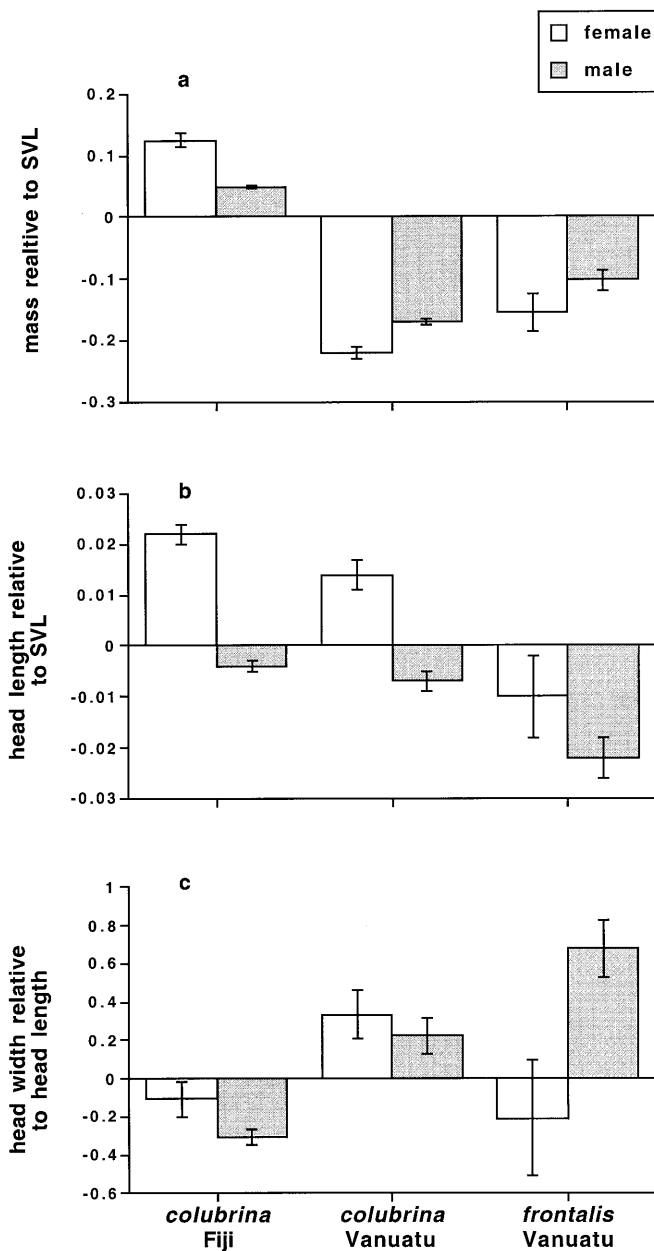


Fig. 3a–c Differences in body proportions as a function of sex and species for the sea-snakes *Laticauda colubrina* (populations from Vanuatu and Fiji) and *L. frontalis* (from Vanuatu). The graphs show mean values and associated standard errors for residual scores from general linear regressions of log-transformed variables: **a** mass relative to SVL; **b** head length relative to SVL; and **c** head width relative to head length. See text for statistical analyses of these data; note that all analyses were based only on snakes <90 cm SVL

Proportion of snakes containing prey

We recorded 59 of 160 *L. colubrina* with prey in the stomach. Three juvenile snakes each contained two prey items, and one contained three. Only 10 of 44 *L. frontalis* contained prey, but one adult male had two prey items and another had five (Table 2). Overall, we found prey in similar frequencies in *colubrina* and *frontalis* ($\chi^2=0.10$,

$df=1$, $P=0.75$). Contingency-table analysis shows that the proportion of snakes containing prey was higher in juveniles than in adults (sexes combined) in *colubrina* ($\chi^2=11.36$, $df=1$, $P=0.0007$) but not in *frontalis* ($\chi^2=0.00$, $df=1$, $P=1.00$). Adult male snakes contained prey less often than adult females in both species, with this trend attaining statistical significance in *colubrina* (11 vs. 35%; $\chi^2=5.99$, $df=1$, $P=0.01$) but not in *frontalis* (17 vs. 33%; $\chi^2=0.50$, $df=1$, $P=0.48$). Thus, the overall pattern was for a relatively high proportion of feeding records from juvenile snakes and adult females, but a low proportion from adult males (Table 2). Logistic regression with sex, species and \ln SVL as independent variables, and “fed or not” as the dependent variable, showed that feeding frequency was affected by body size ($\chi^2=7.66$, $df=1$, $P=0.006$) and sex ($\chi^2=11.54$, $df=1$, $P=0.001$) but did not differ between species ($\chi^2=1.82$, $df=1$, $P=0.18$).

Prey species

Table 2 shows the taxonomic identity of prey items recovered from the stomachs of snakes. All items were eels, mostly morays (Muraenidae, $n=69$) but with occasional congers (Congridae, $n=6$). Conger eels were much larger on average than were morays (means of 24.8 vs. 11.6 mm diameter: $F_{1,73}=46.57$, $P=0.0001$), and the only snakes that consumed conger eels were female *colubrina* >84 cm SVL. Logistic regression shows that whether a snake contained a conger or a moray eel was affected by the snake’s body size: larger snakes took congers (log-likelihood ratio test, $\chi^2=18.05$, $df=1$, $P=0.0001$).

Although both species and all age/sex classes of laticaudines fed exclusively on eels, the detailed dietary composition differed among these groups. All species of prey taken by the smaller species (*frontalis*) were also taken by juveniles or adult males of the larger taxon (*colubrina*), but none of these eel taxa were taken by the much larger adult females of *colubrina* (Table 2).

Prey size

We recorded a wide size range of eels (5.7–41.3 mm body diameter) from the stomachs of laticaudines in Vanuatu. A two-factor ANOVA with sex and species as factors, and prey diameter as the dependent variable (adult snakes only) showed that prey items were larger in females than in males ($F_{1,26}=24.07$, $P=0.0001$), and larger in *colubrina* than in *frontalis* ($F_{1,26}=37.02$, $P=0.0001$). There was no significant interaction between these factors ($F_{1,26}=0.12$, $P=0.74$).

Unsurprisingly, prey size increased with snake body size (Fig. 4). We conducted a two-factor ANCOVA on these data with sex and species as factors, \ln SVL as covariate, and $\log(1 + \text{prey diameter})$ as the dependent variable. This analysis showed that prey size increased with snake size more rapidly in *colubrina* than in *frontalis* (interaction between species and \ln SVL, $F_{1,67}=4.91$,

Table 2 Numbers and sizes of each prey species recorded from stomachs of the sympatric sea-krait species *Laticauda colubrina* and *L. frontalis* in Vanuatu

	<i>L. colubrina</i>			<i>L. frontalis</i>		
	Juveniles	Males	Females	Juveniles	Males	Females
Feeding frequency						
Number of snakes without prey	71	74	15	5	20	8
Number of snakes with prey	42	9	8	2	4	4
Total number of prey items	44	10	8	2	9	4
Prey size						
Mean prey diameter (mm)	10.9	14.5	24.9	11.5	8.2	13.1
Range of prey diameters (mm)	6.3–18.7	12.1–18.8	18.8–41.3	9.0–13.9	5.7–16.4	
Prey types						
Family Congridae						
<i>Conger cinereus</i>	2	0	4	0	0	0
Family Muraenidae						
<i>Echidna delicatula</i>	8	0	0	0	0	0
<i>Enchelycanassa cf. canina</i>	1	0	0	0	0	0
<i>Gymnomuraena zebra</i>	0	0	1	0	0	0
<i>Gymnothorax chilospilus</i>	2	0	0	1	0	0
<i>Gymnothorax enigmaticus</i>	0	0	1	0	0	0
<i>Gymnothorax fimbriatus</i>	3	0	0	0	0	0
<i>Gymnothorax margaritophorus</i>	0	1	0	0	0	0
<i>Gymnothorax undulatus</i>	3	1	1	0	0	0
<i>Gymnothorax cf. buroensis</i>	2	0	0	0	0	0
<i>Gymnothorax cf. gracilicauda</i>	3	2	0	0	2	0
'large mottled' <i>Gymnothorax</i> sp.	0	0	1	0	0	0
<i>Gymnothorax</i> spp.	10	2	0	0	0	0
<i>Scuticaria tigrina</i>	0	1	0	0	0	1
<i>Uropterygius polyspilus</i>	0	0	0	0	0	1
'Plain brown' eel	3	0	0	0	6	0
'Barred greenish' eel	1	1	0	1	0	1
Unknown eel	6	2	0	0	1	1
Total	44	10	8	2	9	4

$P=0.03$). This result was not simply due to differences in relative head-size between the species (*colubrina* have larger heads at the same SVL: see Fig. 3), because the same result was obtained if we used ln head length rather than ln SVL as the covariate ($F_{1,67}=10.80$, $P=0.002$).

To clarify the nature of this effect, we calculated a measure of prey size relative to snake size (residual scores from the linear regression of ln prey diameter versus ln SVL) and performed two-factor ANOVA (with sex and species as factors) on this size-adjusted variable. The analysis revealed a significant interaction term ($F_{1,71}=7.70$, $P=0.007$). Relative prey size was larger in females than in same-sized males in both species, but the difference was greater in *frontalis* than in *colubrina*. When we analyzed data separately by sex, relative prey sizes were similar in females of the two species ($F_{1,35}=1.47$, $P=0.23$) but larger for male *colubrina* than for male *frontalis* ($F_{1,36}=9.21$, $P=0.005$). This pattern is also evident in Table 2, where the mean prey size recorded from adult male *frontalis* was smaller than for any other group (including juveniles of either species).

Comparisons with a Fijian population of *Laticauda colubrina*

We now compare our Vanuatu data with information from a recent study of Fijian *L. colubrina* (Shetty 2000; Shetty and Shine 2001). To enable direct statistical comparisons, we used the raw data from the Fijian study. The data from Fiji were incorporated into a set of analyses identical to those described above except that they included three taxa not two. For analyses of all traits except mean adult SVL, we deleted data for snakes ≥ 90 cm SVL to ensure overlap of body sizes among the species and sexes. Our analyses showed that:

1. Mean SVLs of adult snakes were similar for *colubrina* in Fiji and Vanuatu (males, 82.1 vs. 78.1 cm; females, 114.6 vs. 116.7 cm). The degree of sexual size dimorphism was lower in Fiji than in Vanuatu (0.40 vs. 0.50), but both were much higher than in *frontalis* (0.14).
2. Fijian *colubrina* were more heavy-bodied than Vanuatu conspecifics, with *frontalis* intermediate in this respect (ANOVA on residual scores of ln mass versus ln SVL; species effect $F_{2,914}=695.1$, $P=0.0001$, all post-hoc comparisons $P=0.0001$). The dotted line in Fig. 2 shows the calculated regression for Fiji speci-

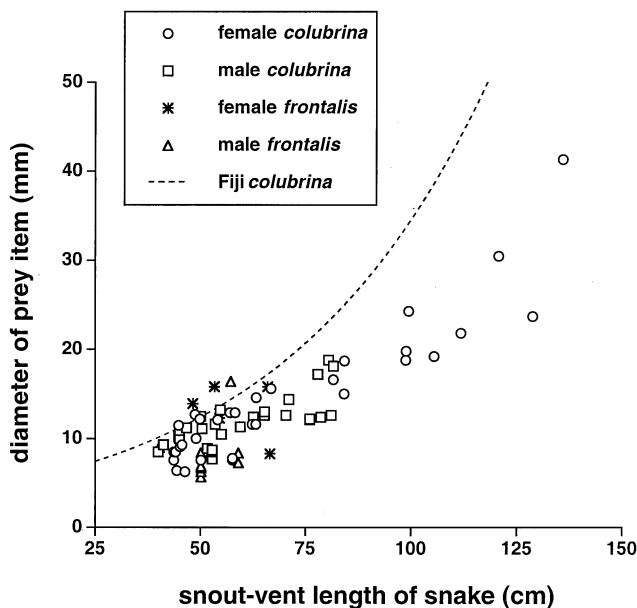


Fig. 4 The body sizes (midbody diameters) of the eels consumed by laticaudine sea-snakes, compared to the body sizes (snout-vent lengths) of the snakes that had consumed them. Data are shown separately for male and female specimens of the sea-snakes *Laticauda colubrina* and *L. frontalis*. The dotted line shows calculated line of best fit to data from Fijian specimens of *L. colubrina*, from Shetty (2000)

mens. However, a strong interaction was evident between sex and species: females were more heavy-bodied than males in the Fijian population, whereas the reverse was true for both of the Vanuatu samples (interaction $F_{2,914}=37.93$, $P=0.0001$).

3. Fijian *colubrina* had longer heads relative to SVL than did the Vanuatu *colubrina*, and *frontalis* heads were shorter still (ANOVA on residual scores from the linear regression of \ln head length on \ln SVL; $F_{2,907}=19.12$, $P=0.0001$, post-hoc tests show that *frontalis* differs from both *colubrina* samples at $P=0.0001$). Female snakes had relatively longer heads than conspecific males in all three samples ($F_{2,907}=42.75$, $P=0.0001$), with a similar degree of sexual dimorphism in relative head length among the groups (interaction $F_{2,907}=1.82$, $P=0.16$; see Fig. 3).
4. Head shape differed between the populations, with heads of the Fijian animals more elongate (i.e. longer relative to width) than those of either Vanuatu taxon ($F_{2,907}=12.57$, $P=0.0001$). Heads of male *frontalis* were much less elongate than were those of conspecific females, whereas the reverse was true for *colubrina* (interaction $F_{2,907}=4.21$, $P=0.015$; see Fig. 3c).
5. Fijian *colubrina* averaged 23 mid/body scale rows in both sexes (Guinea 1986), Vanuatu had 25 (female) or 23 (male), and *frontalis* had 21 (both sexes). Thus, the Vanuatu *colubrina* were the only group to display sex differences in midbody scale counts.
6. Prey size was larger in Fiji than in Vanuatu, in terms of absolute diameters of ingested eels. The difference was twofold in terms of eel diameter (means of 26.8

vs. 13.7 mm) if all prey items were included. Even restricting analysis to prey in snakes <90 cm SVL, the geographic difference in mean eel diameters was considerable (18.4 vs. 11.9 mm; $F_{1,104}=27.34$, $P=0.0001$). The same was true of eel diameter relative to snake SVL: the eels taken by Fijian snakes were larger than those swallowed by Vanuatu snakes at the same SVL (ANOVA on residual scores from the linear regression of $\log(1 + \text{prey diameter})$ versus SVL, species/locality effect $F_{2,131}=27.90$, $P=0.0001$). Post-hoc tests confirmed that the two Vanuatu species consumed smaller prey (relative to their own SVL) than did the Fijian animals ($P<0.03$; see dotted line in Fig. 4 for Fiji data).

Discussion

Our data show that the range of body sizes (diameters) of eels consumed by our Vanuatu sea kraits was lower than in a previously-studied Fijian population of one of these snake species. This difference reflects the scarcity of large conger eels within the Vanuatu snakes. It is possible that this scarcity is due to active rejection of large prey items by the Vanuatu sea-kraits (for some unknown reason), but a simpler and more likely explanation (supported by our observations from diving) is that large eels are less common in Vanuatu than in the Fijian study area. The geographic difference in mean prey sizes was twofold in terms of prey diameter, and would be much greater in terms of prey mass. The apparent scarcity of large prey items in Vanuatu appears to have had several consequences:

1. Feeding rates of the Vanuatu snakes were similar to those of snakes in Fiji, with adult males feeding less frequently than other groups within the population (probably due to anorexia during the breeding season: Shetty 2000; Shetty and Shine 2001). However, the eels that were consumed by the Vanuatu snakes were small not only in absolute terms, but also relative to snake size.
2. Perhaps reflecting this lowered rate of food intake, the Vanuatu snakes were more slender-bodied than the Fijian animals. This was particularly true for adult female *colubrina*, the group for which the prey resource was probably most different between the two areas. Without experimental data, we do not know if the more slender body form of the Vanuatu animals is a simple proximate effect (lower energy stores) or an adaptation (for example, to enter narrow crevices while foraging).
3. Despite the lower resource base in Vanuatu, *colubrina* in this area attain similar mean adult SVLs as their Fijian conspecifics. Some snake species display dramatic geographic variation in mean body sizes as a function of differences in prey resources (e.g. Schwaner and Sarre 1990; Madsen and Shine 1993). This trend appears interspecifically rather than intra-

specifically in our data: the endemic Vanuatu species (*frontalis*) is much smaller than *colubrina*. Such dwarf forms have evolved at least three times within laticaudine phylogeny (*crockeri*, *frontalis*, *schistorhynchus*: Cogger et al. 1987; Heatwole and Guinea 1993), perhaps reflecting the importance of prey size (and thus, body size) as an axis of ecological variation within the group.

4. The degree of SSD was lower in *colubrina* from Vanuatu than in conspecifics from Fiji, and lower still in *frontalis*. This might reflect a direct effect of lower food supply for large female snakes, and fits well with the observation that the Vanuatu snakes were thinner-bodied than their Fijian counterparts. The lower SSD in the Vanuatu animals is consistent with the prediction that a restricted range of prey sizes will cause a decrease in SSD (Slatkin 1984; Forsman 1991b; Madsen and Shine 1993). Potentially, SSD could be generated either by sex differences in growth trajectories or by sex differences in survival rates (and thus, ages). Extensive mark-recapture data on the Fiji population of *L. colubrina* reveal that the former process is most important in that system (Shetty and Shine 2001). The disparity in the degree of SSD between the two Vanuatu laticaudines can best be appreciated by comparison with the range seen in other snake species. Of the 377 species for which data are available (from Shine's 1994 review plus the two Vanuatu taxa), *colubrina* would rank as No.375 and *frontalis* as No.285. Allometric shifts in the degree of SSD among snakes complicate interpretation of this divergence, however (Shine 1994; Shine et al. 1998).
5. Intraspecific and interspecific variation in relative head lengths of snakes have been interpreted as adaptations to differing prey sizes (e.g. Forsman 1991a). We saw the same shift within our sea kraits, with relative head lengths mirroring relative prey sizes (i.e. Fiji *colubrina* > Vanuatu *colubrina* > *frontalis*).
6. The direction and degree of sexual dimorphism in relative head length was conservative, but with complex shifts in head shape (width relative to length). Notably, male *frontalis* had exceptionally short, wide heads (Fig. 3), and also consumed smaller prey items (on average) than did any of the other groups (Table 2).
7. The three laticaudine taxa showed clear differences both in the number of midbody scale-rows, and in their degree of dimorphism in this trait. Higher numbers of mid-body scale rows may facilitate the ingestion of relatively larger prey (Mell 1929; Pough and Groves 1983; Shine 2002). This hypothesis is consistent with the small prey taken by *frontalis* and by male rather than female *colubrina* in Vanuatu, but is not consistent with the higher scale count of female *colubrina* in Vanuatu versus Fiji.

The most general patterns in our data are that: (1) we found geographic variation in mean adult body sizes and in the degree of sexual dimorphism in body size and relative head size, as expected if these traits are sensitive to

the spectrum of available prey sizes; (2) in most respects, *colubrina* from Vanuatu are intermediate between Fijian *colubrina* and *frontalis* in traits such as body sizes, degree of sexual dimorphism, and mean prey sizes; we suggest (but cannot show) that the attributes of Vanuatu *colubrina* might largely reflect phenotypic plasticity whereas those of *frontalis* reflect adaptation; and (3) some traits (such as the sex divergence in head lengths relative to SVL) were highly conserved, despite major shifts in mean adult body sizes, SSD, and prey sizes relative to body size. Other traits (such as sex divergence in head shape) were more variable.

Although it is difficult to infer the processes at work in generating this intraspecific and interspecific diversity within laticaudines, we found strong correlations between sexual dimorphism and prey spectra within these snakes. In a habitat where large prey items appear to be less abundant, the Vanuatu sea-snakes display small body sizes and a reduced degree of sexual size dimorphism. Most dramatically, we see the evolution of a dwarf form (*frontalis*) that exploits the prey-size niche of juvenile and adult male (but not adult female) *colubrina*. Such shifts in adult body size and the degree of sexual dimorphism fit well with mathematical models that relate prey-size distributions to the evolution of sexual dimorphism in gape-limited predators (Slatkin 1984). It may well be that sexual selection and/or fecundity selection were the initial selective forces for the evolution of SSD in laticaudines (Shine 1994), but our data from Vanuatu suggest that niche divergence between the sexes has acted as an additional influence on sexual dimorphism in snakes of this lineage.

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