

# Sexual divergence in diets and morphology in Fijian sea snakes *Laticauda colubrina* (Laticaudinae)

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**Abstract** In the Fiji Islands, female yellow-lipped sea kraits (*Laticauda colubrina*) grow much larger than males, and have longer and wider heads than do conspecific males of the same body length. This morphological divergence is accompanied by (and may be adaptive to) a marked sex divergence in dietary habits. Adult female sea kraits feed primarily on large conger eels, and take only a single prey item per foraging bout. In contrast, adult males feed upon smaller moray eels, and frequently take multiple prey items. Prey size increases with snake body size in both males and females, but the sexes follow different trajectories in this respect. Female sea kraits consume larger eels relative to predator head size and body length than do males. Thus, the larger relative head size of female sea kraits is interpreted as an adaptation to consuming larger prey items. Our results are similar to those of previous studies on American water snakes (natricines) and Australian file snakes (acrochordids), indicating that similar patterns of sex divergence in dietary habits and feeding structures have evolved convergently in at least three separate lineages of aquatic snakes.

**Key words:** convergent evolution, dimorphism, feeding habits, Fiji Islands, sea kraits.

## INTRODUCTION

Ecomorphological studies have documented strong links between an animal's feeding habits (the size and shape of prey items that it consumes) and its trophic structures (the size and shape of the apparatus that it uses to handle those prey items (Schwenk 2000)). However, the correlation between these two aspects is less than perfect, for several reasons. First, phylogenetic history can constrain the morphology of trophic structures, such that shifts to novel prey items are not reflected in morphological adaptations (Gould 1980; Harvey & Pagel 1991). Second, a general-purpose feeding morphology may be able to accommodate a diverse range of prey types. For example, a predator that reduces its prey items to small pieces prior to ingesting them will not require modifications of ingestion systems for different prey sizes (Schwenk 2000). Third, organisms often use their trophic structures (such as teeth) for purposes other than feeding (e.g. defence against predators; battles against conspecific rivals) and thus adaptations to these competing functions may constrain adaptations related to foraging efficiency (Shine 1989).

For these reasons, studies on the relationship between trophic structures and dietary habits may best be pursued with organisms that (i) differ in diets despite being very closely related to each other; (ii) are

gape-limited predators, such that an increase in prey size requires substantial morphological modification to the predator; and (iii) do not use their trophic structures in conspecific rivalry or antipredator displays. One system that fulfils these conditions, and hence provides ideal opportunities for research on this topic, is sexual dimorphism in snakes. Empirical studies on snakes have provided clear evidence of sexual divergences in food habits (reviewed by Shine 1991b). By restricting comparison to the two sexes within a single population, confounding issues are minimized (Temeles *et al.* 2000). Because many snakes eat prey items that are large relative to the size of the predator, and must be swallowed entire, head dimensions constrain maximal ingestible prey sizes (Mushinsky 1987). Last, male–male agonistic interactions in snakes typically do not involve use of the jaws (Carpenter 1986). Thus, sexual dimorphism in feeding structures and diets in snakes may provide a unique opportunity to investigate the ways in which subtle differences in dietary habits can favour the evolution of intraspecific shifts in feeding morphology (Shine 1991a,b).

In some snake species, dietary divergence between males and females is likely to be a simple reflection of sex differences in adult body size (Madsen 1987; Shine *et al.* 1998). In other cases, however, the sex based dietary divergence is accompanied by significant dimorphism in head morphology. Two of the best examples of this latter phenomenon involve aquatic snakes. In two distantly related lineages (natricines and acrochordids), occupying very disparate areas (North

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America and Australia), females grow larger than males, take larger prey items, and have disproportionately larger jaws (Mushinsky *et al.* 1982; Shine 1991a,b; Houston & Shine 1993). Anecdotal reports suggest that the same phenomenon may have evolved independently in yet another species of aquatic snake, the yellow-lipped sea krait *Laticauda colubrina*. Measurements of preserved specimens documented larger head sizes in females than males (Camilleri & Shine 1990), and limited field studies hint at a sex-based difference in dietary habits (Pernetta 1977). However, detailed field studies to clarify this issue have not been conducted on *Laticauda*, nor on any species of sea snake (Heatwole 1999). To determine whether or not these snakes have indeed evolved the same kind of sex-based niche partitioning as described in natricine and acrochordid taxa, we carried out a detailed ecological study of sea kraits in the Fiji Islands.

## METHODS AND STUDY SITES

### Study sites

Our field study was conducted between September 1998 and December 1999, on two islands in the Bau waters (Tailevu Province). Mabualau (also known as Bird Island; 178°46'E, 17°58'S) lies approximately 6 km off the south-east coast of Viti Levu, and approximately 25 km from the city of Suva. It is a 4-ha limestone islet with a maximum height of 5 m above sea level, and is surrounded by shallow reef flats. Toberua is a sandy resort island 5.3 km from the (generally uninhabited) Mabualau. It is approximately 1.5 ha in area, and rises approximately 2 m above sea level. Like Mabualau, it has a vast (> 40 ha) expanse of fringing reef flats, which are exposed during low tide.

### Methods

Snakes from both islands were collected by hand, either on land or in shallow water close to land, and brought to our camp-site for processing.

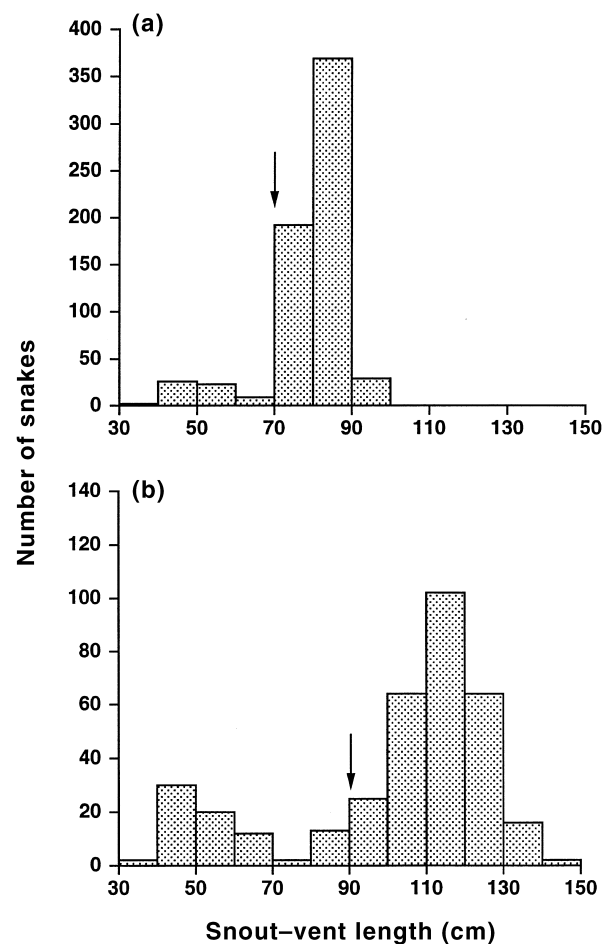
### Sexual dimorphism

We measured snout-vent length (SVL,  $\pm 1$  cm) using a measuring tape, and head dimensions (length and width,  $\pm 1$  mm) using Vernier callipers. Head width was measured at the widest part of the head. Head length was measured along the jaw, from the tip of the snout to the back of the mandibular joint. The sexes of *L. colubrina* are easily distinguished. Females have short, thin, flattened tails, whereas males have long pear-shaped, fleshy tails. Based on dissections of Fijian

*L. colubrina*, Guinea (1986) reported that males mature at 70 cm SVL and females at 90 cm. Thus, we classified males and females with SVL > 70 and 90 cm, respectively, as adults. Individuals were marked by scale-clipping and released near our campsite. Because we recaptured many of these animals after approximately 12 months, we could assess the repeatability (and ontogenetic stability) of measures such as relative head length.

### Diet sampling

The stomach of every snake was squeezed gently to locate prey items. If present, these were removed by palpation (Shine 1986; Fitch 1987). Because these snakes feed exclusively on eels, the prey were easily and rapidly regurgitated. We recorded the number of prey items, the family to which they belonged, maximum diameter of the prey and their orientation (swallowed head-first or tail-first).



**Fig. 1.** Frequency distributions of snout-vent length for (a) male and (b) female sea kraits from Mabualau and Toberua Islands, Fiji. Sizes at sexual maturation in each sex are indicated by arrows.

## RESULTS

Of the 1138 snakes we measured, 810 were from Mabualau and 328 were from Toberua. Data from these two locations were combined for the following analyses.

### Sexual dimorphism

Adult male and female *Laticauda colubrina* differed significantly in SVL, head length and head width. Females grew much larger than males, and had longer heads (Figs 1,2). We can then ask whether females exceed males in head size simply because they grow larger overall. To remove the confounding effect of body size on head dimensions, we excluded data from snakes > 95 cm SVL in order to ensure body size overlap of males and females (Fig. 2). Data on the remaining snakes were used in one-factor ANCOVA with sex as the factor, SVL as the covariate, and the natural log of head length or head width as the dependent variable. We ln-transformed head dimensions (but not SVL) for these tests to obtain linear relationships between SVL and head dimensions. Inspection showed significant curvilinearity in regressions based on untransformed values (Fig. 2) and in regressions based on ln-transformed values for both variables. Relative head sizes shift in complex ways during sea-krait ontogeny, such that the regression of ln head length versus SVL offers the best linear relationship ( $r \geq 0.89$  for all regressions).

The ANCOVA shows that males and females differed in head size even after the effects of overall SVL were factored out of the analysis. Head lengths were larger in females than in males at the same SVL ( $F_{1,710} = 77.62$ ,  $P < 0.0001$ ; slopes homogeneous

$F_{1,709} = 0.29$ ,  $P = 0.59$ ); that is, females are born with larger heads, and maintain this difference throughout life. Head width increased faster with increasing SVL in female sea kraits than in males (heterogeneity of slopes test,  $F_{1,709} = 4.32$ ,  $P < 0.04$ ).

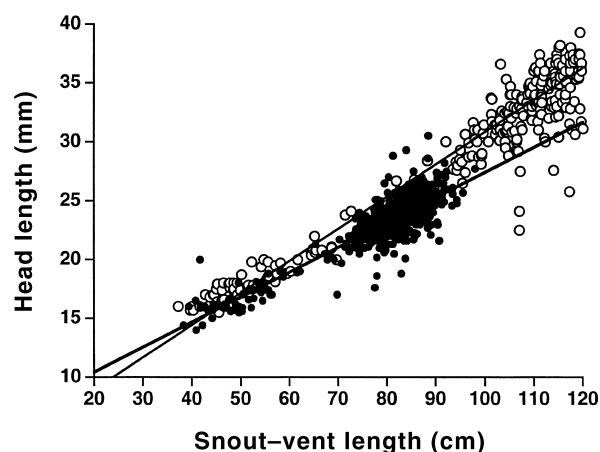
The repeatability and ontogenetic stability of relative head sizes are most easily examined using residual scores from general linear regressions of ln head size versus SVL for each sex. Comparing residual scores from measurements taken in late 1998 versus those on the same snakes in late 1999, we detected highly significant repeatabilities for both relative head length (for 61 females,  $r = 0.58$ ,  $P < 0.0001$ ; for 292 males,  $r = 0.40$ ,  $P < 0.0001$ ) and relative head width (for 61 females,  $r = 0.57$ ,  $P < 0.0001$ ; for 292 males,  $r = 0.43$ ,  $P < 0.0001$ ). That is, snakes that had unusually long or wide heads (relative to other snakes of the same sex) in 1998 still had unusually long or wide heads when recaptured a year later.

### Feeding habits

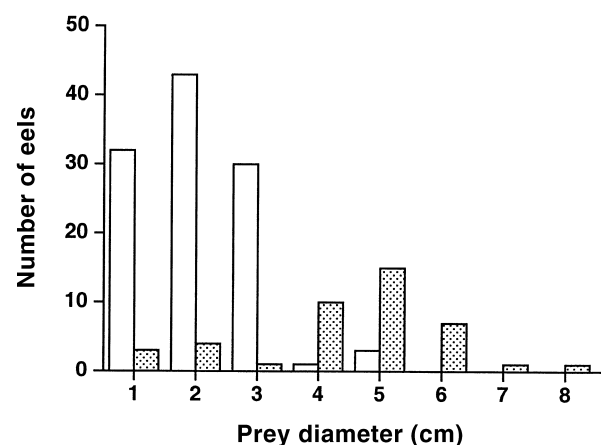
All of the prey items that we palpated from *L. colubrina* were eels belonging to two families, the Muraenidae (moray eels) and the Congridae (conger eels). Of 113 snakes that were examined for the orientation of prey items, 64% had consumed their prey head first and the remaining 36% had consumed prey tail first.

#### Proportion of snakes containing food

Among a total of 860 adult snakes, 11.7% of females (32 of 273) had prey items in their stomachs, compared with only 3% of males (18 of 587:  $\chi^2 = 25.49$ , 1 d.f.,  $P < 0.0001$ ). If we restrict analysis to the range of common body sizes (SVL < 95 cm, including juveniles as well as adults), the proportion of snakes with prey



**Fig. 2.** Head length relative to snout-vent length (SVL) in (●) male and (○) female sea kraits. See text for statistical analysis based on ln-transformed head length versus SVL; untransformed values are plotted here.



**Fig. 3.** The size (body diameter) distributions of (□) moray ( $n = 112$ ) and (▨) conger ( $n = 42$ ) eels consumed by sea kraits.

in their stomachs was 26.7% of females (23 of 86) and 9.3% of males (58 of 627;  $\chi^2 = 21.28$ , 1 d.f.,  $P = 0.0001$ ). Thus, females contained prey more frequently than males.

#### Prey types

Prey types and sizes were strongly correlated, because conger eels were generally larger than moray eels (Fig. 3;  $F_{1,75} = 61.57$ ,  $P < 0.0001$ ). Larger snakes consumed larger eels (regression of snake SVL versus prey diameter, including snakes of all body sizes:  $n = 158$ ,  $r = 0.86$ ,  $P < 0.0001$ ). Thus, conger eels were found more often in adult snakes, whereas gut contents of juvenile snakes comprised mostly moray eels ( $\chi^2 = 25.48$ , 1 d.f.,  $P < 0.0001$ ). Similarly, many conger eels were eaten by female snakes, whereas male snakes fed mostly on moray eels ( $\chi^2 = 60.57$ , 1 d.f.,  $P < 0.0001$ ; see Fig. 4). Hence, both age class and sex appear to influence a sea krait's diet. These factors are themselves linked (because of sex differences in body size), so we examined the effects of sex on dietary habits within adult and juvenile snakes separately. Contingency-table analyses revealed significant effects of sex on dietary composition within both adult ( $\chi^2 = 45.51$ , 1 d.f.,  $P < 0.0001$ ) and juvenile ( $\chi^2 = 7.65$ , 1 d.f.,  $P = 0.0057$ ) sea kraits. These sex differences took the same form in both age classes of snakes: conger eels were consumed more often by females, whereas males consumed more moray eels (Fig. 4).

#### Prey sizes

Female sea kraits consumed larger prey items than did males, within juvenile snakes (means of 1.97 vs

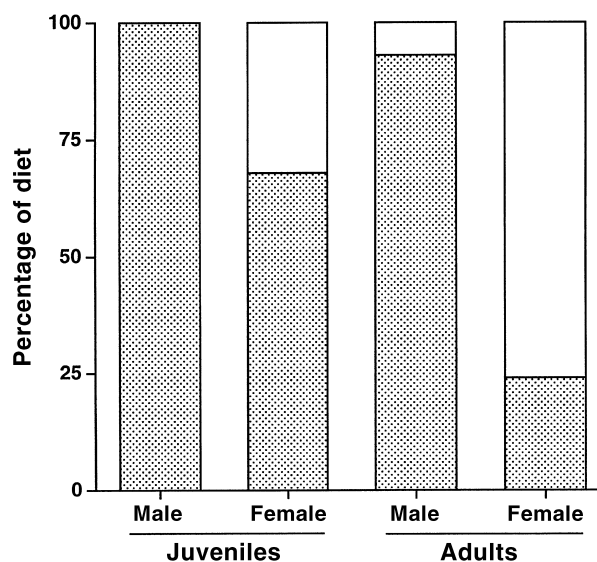


Fig. 4. Relative importance of (■) moray and (□) conger eels in the diets of sea kraits, as a function of the sex and age class of the snake.

1.22 cm;  $F_{1,62} = 13.80$ ,  $P < 0.0004$ ) as well as adults (means of 4.37 vs 2.05 cm;  $F_{1,47} = 91.96$ ,  $P < 0.0001$ ). We asked whether these differences in prey size between the sexes could be attributed simply to body-size differences. To investigate this question, the data were limited to snakes with SVL < 95 cm so as to ensure size overlap between the sexes. A one-factor heterogeneity of slopes test was conducted with prey size as the dependent variable, sex as the factor and SVL as the covariate. Prey size was significantly affected by the interaction between sex and body size ( $F_{1,116} = 12.29$ ,  $P = 0.0006$ ). That is, the rate at which prey size increased with a snake's SVL was greater in females than in males (Fig. 5). We then repeated the analysis using head length rather than SVL as the covariate, again restricting the data set (head length < 30 mm) to ensure overlap between the sexes. The interaction between sex and head length was significant ( $F_{1,116} = 15.02$ ,  $P = 0.0002$ ). The same result was obtained when head width rather than length was used as the covariate ( $F_{1,116} = 8.59$ ,  $P < 0.005$ ).

These analyses show that prey size increased with a snake's head size more rapidly in females than in males (Fig. 5). However, they do not necessarily mean that females eat larger prey than males of the

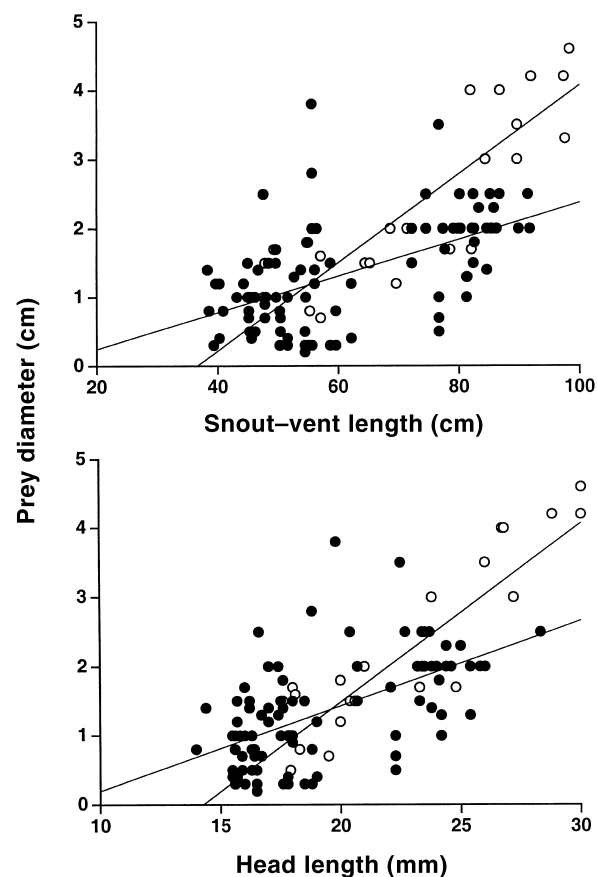


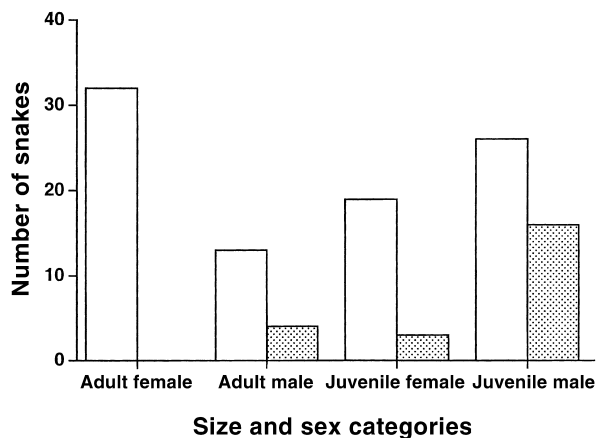
Fig. 5. Relationship between prey size and snake body length (SVL, upper graph) or head size (lower graph) in (●) male and (○) female sea kraits.

same body size. Indeed, the largest prey items for any given snake SVL were often from males, because sample sizes were larger for males than for females (Fig. 5). Analysis reveals a general pattern of females eating larger prey, but with the prey-size disparity between the sexes increasing in larger snakes. If we divide the snakes into 10-cm SVL categories, we find that mean prey diameter was greater for females than for males in each of these categories. However, the sex difference in mean prey diameter was smaller in smaller snakes (on average, prey were 19% larger in females than in males for sea kraits < 70 cm SVL, but 51% larger for snakes from 70 to 90 cm SVL).

These analyses suggest that female sea kraits eat larger prey items than males partly because of the larger body size of females, and partly because of the larger relative head size of females compared with males. However, even after these morphological factors are removed from the analysis, a difference remains. That is, female sea kraits eat larger prey items (on average) than do males, even if we restrict attention to snakes of identical head sizes (Fig. 5).

#### *Numbers of prey items per meal*

Recently fed snakes of various sex and size classes differed significantly in the numbers of prey items that they had ingested ( $\chi^2 = 17.05$ , 3 d.f.,  $P = 0.0007$ ). All of the adult female sea kraits examined had only one prey item in their gut (or none), whereas multiple prey items were recorded in adult male and juvenile snakes (Fig. 6). Again, if we compare males and females over the same range of body sizes (SVL < 95 cm), the sex difference remains ( $\chi^2 = 5.45$ , 1 d.f.,  $P = 0.02$ ; 11% of females had more than one prey item, compared with 35% of males).



**Fig. 6.** Number of snakes (adults and juveniles of each sex) containing (□) single versus (▨) multiple prey items.

## DISCUSSION

Sex-based divergence in feeding habits and trophic structures has been reported in a wide variety of animal species (Shine 1989; Temeles *et al.* 2000). Snakes offer some of the best examples of this phenomenon, and *L. colubrina* is among the most dramatic of these examples. Our data confirm previous reports that male and female yellow-lipped sea kraits differ not only in mean adult body length (Saint Girons 1964; Guinea 1986), but also in relative head size (Camilleri & Shine 1990; Shine 1991a,b), and in the sizes and types of prey that they consume (Pernetta 1977). In all these respects, *L. colubrina* provides a striking parallel with the situation recorded for American water snakes (Mushinsky 1987) and Australian file snakes (Houston & Shine 1993). Although the three taxa involved are only distantly related, and represent independent evolutionary invasions of aquatic habitats, they share remarkable similarities in terms of sexual dimorphism. Females grow larger than males in all three cases, have larger heads relative to body size, and feed on larger fishes than do conspecific males. The similarities extend to more specific points, such as a lower incidence of multiple prey in females than males.

#### Adult body size

First, we consider the sex difference in mean adult body size. The degree of sexual size dimorphism in a population reflects the end result of competing selective pressures acting independently in the two sexes (Andersson 1994). Sex differences in body size are widespread in snakes, and generally take the form of females growing larger than conspecific males (Shine 1978, 1993, 1994), as is the case in sea kraits. However, the degree of sexual dimorphism in *L. colubrina* is greater than that in most other snakes. Using the system of Gibbons and Lovich (1990), the mean degree of sexual size dimorphism in the sea kraits from our study area is 0.394. That is, adult females were on average 39.4% longer than adult males. This value is exceeded by only 10 of the 375 snake species reviewed by Shine (1994). Because mass increases rapidly with increasing SVL, the degree of sexual dimorphism would be much greater if calculated in terms of mass rather than body length.

The reasons why female sea kraits grow so much larger are likely to be complex, involving three processes:

1. Fecundity selection may favour large body size in females, because of enhanced reproductive output (Seigel & Ford 1987). In keeping with this hypothesis, larger female sea kraits produce larger clutches (Gorman *et al.* 1981; Guinea 1996).
2. Sexual selection on body size in males may favour small size in this sex, or at the very least provide

no advantage to larger body size. In snake species that display overt male–male combat, larger males tend to win the battles and thus obtain more opportunities for mating (Schuett & Gillingham 1989; Madsen & Shine 1993; Schuett 1997). The same may be true, to a lesser degree, in many snake species where males scramble physically for mating opportunities but do not show ritualized combat (Madsen & Shine 1993; Luiselli 1996; Shine *et al.* 2000). However, our observations of mating groups of *L. colubrina* provided no evidence of any vigorous physical interactions among competing males. Crucially, male sea kraits that copulated were no larger than those that did not (Shetty 2000; Shetty & Shine 2001). Thus, male sea kraits may not be under any sexual selection for larger body size. Indeed, smaller body size might benefit a male by enabling him to resist a long period of fasting associated with reproductive activity, as seen in other snake species (Shine 1980; Mushinsky 1987). In our study, adult male sea kraits rarely contained prey items. Our work was conducted during the snakes' mating season (Shetty 2000; Shetty & Shine 2001), so that anorexia by reproductive males might explain the sex difference in frequency of feeding.

3. Natural selection may have reinforced the size dimorphism originally generated by fecundity selection. Body size can affect many aspects of an organism's biology, including its locomotor performance (Jayne & Bennett 1990; Shine & Shetty 2001). As in acrochordids (Houston & Shine 1993), male and female sea kraits diverge not only in dietary habits but probably in foraging habitats as well. The tendency for females to eat very large eels, and for males to specialize on small eels (Fig. 5) may have provided advantages to each sex in developing adaptations to foraging in different places for different kinds of prey. Natural selection of this type could thus amplify existing sex differences in aspects such as body size and relative head size.

### Head size

Our data document a strong difference between male and female sea kraits in head size relative to body length. As in the case of body size dimorphism, such divergence is relatively common in snakes but is rarely so extreme as it is in *L. colubrina*. A previous review of head size divergence between the sexes suggested that *L. colubrina* was among the most extreme such cases (Shine 1991b), and our data reinforce this conclusion. Ecological divergence between sexes offers the most plausible functional basis for the observed divergence in head size. The dimorphism is so extreme that it is

unlikely to have evolved by non-adaptive processes such as neutral allelic substitutions, and there is nothing in the mating system of this species that suggests any role for relative head size in sexual selection (Shetty 2000; Shetty & Shine 2001). Head size in sea kraits almost certainly plays a role in prey handling and ingestion, as indicated by the relationship between prey size and snake size (Fig. 5). It would be physically impossible for a male sea krait to ingest some of the large eels consumed by females. Thus, in this gape-limited predator, selection to ingest larger prey items has presumably played a role in selecting for larger relative head size in females. Smaller heads might enable male sea kraits to reach further into crevices to obtain eels (Radcliffe & Chiszar 1980).

Dietary specialization is widespread in snakes and is associated with the evolution of many modifications of the head for ingesting different types of prey (Cundall 1987). However, intraspecific (sex-based) dietary divergence has attracted much less study than has interspecific divergence in this respect. In many ways, the two sexes of sea kraits are different ecological entities. Females tend to eat conger eels, whereas males and juveniles consume more moray eels. This taxonomic distinction is accompanied by a habitat divergence. Most congeners are found in deep water rather than around reefs, whereas many morays are shallow water species with smaller maximum sizes (Randall *et al.* 1990). Sex differences in dietary habits were previously suggested for *L. colubrina* by Pernetta (1977), but on the basis of a very small sample size ( $n = 13$  prey items).

One of the most interesting aspects of our results is the demonstration that the sexes diverge in prey sizes relative to predator size. This is true even if head size (rather than SVL) is used as the measure of predator body size. That is, the divergence in prey sizes cannot simply be attributed to gape limitation combined with sex differences in relative head size. In combination with our other data, this result suggests that male and female sea kraits have evolved morphological adaptations that suit them to foraging in different areas (shallow *vs* deep water) on different sizes and kinds of eels. Thus, the divergence in head sizes is a consequence rather than a cause of the sex difference in foraging biology.

One puzzling issue, however, is that maximum prey sizes were often larger for male sea kraits than for females at the same SVL (Fig. 5). This result is largely an artefact of the greater sample size for males, but emphasizes that a sex divergence in mean prey sizes may not necessarily result in a divergence in maximum prey sizes. It is difficult to disentangle these two aspects in terms of selective forces. For example, maximum prey size may be the most relevant for gape limitation, but mean prey size may be important in terms of the ease and speed of prey ingestion. It seems likely that a

larger sample size of prey items would reveal that compared with males of the same SVL, females take larger maximum prey sizes as well as larger mean prey sizes. However, we do not have such data.

Our study not only confirms that the sexes of yellow-lipped sea kraits diverge in ecological (dietary) as well as morphological (relative head size) traits, but also shows that the sexes diverge in these aspects even before they reach sexual maturity (Fig. 5). Under the scenario that we propose, the initial selective pressure that generated morphological divergence between the sexes was related to reproductive biology, and hence involved the phenotypic traits of adult snakes. Why, then, does sex affect foraging biology and trophic structures of juvenile snakes? Selection on the traits of adult snakes presumably favoured such extreme ecological and morphological differences between the sexes that in order to display such dimorphism in adult life, males and females must diverge in these respects even in the juvenile stage. Growth rates also differ between the sexes at this stage, with juvenile females growing faster than juvenile males (Shetty 2000). Our study thus reinforces the view that ecological divergence between the sexes can act as a powerful selective force on morphological traits, and hence that patterns of sexual dimorphism are determined by ecological pressures as well as by sexual selection (Shine 1991a,b; Andersson 1994; Temeles *et al.* 2000).

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