



## Determinants of dietary specialization: a comparison of two sympatric species of sea snakes

François Brischoux, Xavier Bonnet and Richard Shine

F. Brischoux (*brischoux@cebc.cnrs.fr*) and X. Bonnet, *Centre d'études Biologiques de Chizé – CNRS, FR-79360, Villiers en Bois, France. FB also at: Univ. François Rabelais, 3 rue des Tanneurs, FR-37041 Tours, Cedex 1, France.* – R. Shine, *Biological Sciences A08, Univ. of Sydney, New South Wales 2006, Australia.*

Why do some predator species specialize on only a single type of prey whereas others take a broad range? One critical determinant may be the ontogenetic range of body sizes of the predator compared to that of its prey. If any single prey taxon spans only part of the range of prey sizes ingestible by the predator, then the predator will be more likely to take multiple prey taxa. We exploit a model system that provides a robust opportunity to test this hypothesis. We studied two sympatric species of predatory sea snakes, similar in size and general ecology that feed on anguilliform fishes from different habitats in the Great Lagoon of New Caledonia. Eel species from soft-bottom habitats must construct their own burrows, and thus tend to be more slender-bodied and less variable in body size than eel species that inhabit variable-sized crevices among hard coral. As a result, a laticaudine sea snake species (*Laticauda saintgironsi*) that feeds on hard-coral-dwelling eels relies primarily on a single prey species: juveniles take young eels whereas adults consume adult eels of the same species. In contrast, a laticaudine species (*L. laticaudata*) that forages on soft-bottom eels switches its prey ontogenetically: juveniles take small eel species whereas adults consume large eel species. Thus, habitat-imposed constraints on the range of body sizes within each prey taxon generate a striking difference in the degree of dietary specialization of two closely related, sympatric predator species.

Understanding the factors that shape each species' niche remains a major challenge for ecological theory (Tokeshi 1999). One of the most fundamental questions concerns dietary breadth: why are some organisms specialized to feed on only one or a few species of prey, whereas closely related organisms take a diverse array of prey taxa? Most lineages of predators include both specialized and generalized taxa in terms of diet breadth (Glodek and Voris 1982, Steenhof and Kochert 1988, Holbrook and Schmitt 1992, Nyffeler 1999, McDonald 2002). There are multiple causal influences on dietary diversity (Peckarsky 1982, Greene 1986), including issues such as foraging mode (sit-and-wait vs active foragers), the presence of competitors (intra and inter specific competition) and the relative abundance and availability of alternative prey species. Dietary specialization may be influenced by individual strategies (Holbrook and Schmitt 1992, Bolnick et al. 2003), foraging experience (Amundsen et al. 1995), sexual dimorphism (Camilleri and Shine 1990), body size (Holbrook and Schmitt 1992, Beaudoin et al. 1999), age, or population density (Svanbäck and Persson 2004). Some of these explanations are specific to particular species, but others may apply more broadly. For example, many models of optimal foraging predict whether predators will add or delete prey types from the diet based on energetic efficiencies (cost/benefit ratio; Schoener 1971, Stephens and Krebs 1986). The assumptions underlying many optimal

foraging models have attracted strong criticism (Pierce and Ollason 1987), and arguments based on currencies other than energy intake may prove to be more useful. For example, in many predator species, the body size of a predator is strongly linked to the size of its prey (Vézina 1985, Arnold 1997). Based on the near-ubiquity of this relationship among snakes and their prey, Shine and Wall (2007) suggested that the intraspecific range in body sizes of the predator compared to its prey species will influence dietary diversity. That is, dietary specialization is likely only if the available range of body sizes of prey within a single prey taxon fills the spectrum of prey sizes potentially used by a snake species. If individuals of any given prey species span only a small size range, snake predators likely will be forced to shift from one prey species to another as they grow larger (Shine and Wall 2007).

Examining ontogenetic shifts in prey types and sizes within predator taxa may yield insights into the determinants of dietary diversity. As a predator grows larger it can increase its prey size either by taking larger specimens of the same prey species, or by shifting from one prey species to another. The former route produces dietary specialization, whereas the latter results in a generalist diet. To explore these issues, a model system would involve a comparison between predator-prey systems that are similar in most important respects. For example, (a) closely related species

of predators exhibiting similar ranges in body sizes to limit allometric complications; (b) sympatric predators, so that environmental conditions are held constant; (c) gape-limited predators that offer an unambiguous causal link between predator size and prey size; (d) predators that consume relatively large prey (Shine and Wall 2007); and (e) a limited morphological diversity in prey, simplifying quantification of 'prey size' (Vincent et al. 2004). Lastly, we need dietary divergence between our predators, accompanied by divergence in the range of body sizes within prey taxa (i.e. one predator species has access to prey of a wide size range within a single prey species, whereas the other predator species takes prey taxa that each encompass only limited intraspecific size variation).

The amphibious sea snakes (sea kraits) of the Great Lagoon of New Caledonia fulfill all of these conditions. In the course of ecological research on insular populations of these snakes, we found that one taxon has a relatively specialized diet (>45% of prey items belong to a single taxon) whereas the other feeds more broadly (no single species constitutes >25% of prey recorded). We note, however, that terms such as 'specialised' and 'generalised' need to be viewed within the context of the group in question. For example, sea snakes tend to have more diverse diets than do terrestrial snakes in closely related lineages (Heatwole 1999). Hence, a marine 'specialist' may feed on a larger number of prey species than does a 'generalist' terrestrial snake. Additionally, a specialist predator may feed heavily on a small number of prey species but nonetheless incorporate many secondary species; whereas a generalist may feed on a lower absolute number of prey species but consume substantial proportions of most of them. That situation can lead to the apparent paradox where a 'specialised' predator actually consumes prey from more species than does a 'generalist' predator. This issue highlights the importance of distinguishing species richness from evenness in diversity estimates. In the current paper, we use the term 'specialist' to refer to a predator that feeds primarily on a small number of prey taxa, and 'generalist' to refer to a predator that take substantial numbers of several different types of prey.

In the current paper we examined ontogenetic shifts in diet of both taxa, to explore the hypothesis that interspecific divergence in the degree of dietary specialization can be explained by relative magnitudes of body-size variation in predators compared to their prey. We predicted that for the specialized predator, a wide size range of the main prey species would be available to all snake size classes. By contrast, some constraint (habitat, prey size . . .) would force the other snake species to shift between different prey taxa as it increases in size.

## Material and methods

### Study species and site

Two sympatric species of sea-kraits are abundant in New Caledonia: *Laticauda saintgironsi* (Cogger and Heatwole 2006) and *L. laticaudata* (Saint Girons 1964, Ineich and Laboute 2002). Neo-Caledonian sea-kraits forage in the lagoon where they feed on more than 50 species of fishes,

mostly anguilliform taxa (moray-eels, snake-eels and conger-eels; Ineich et al. 2007). The snakes forage along the lagoon floor, exploring cavities and burrows in search of sheltering fish. After a successful foraging trip that generally lasts about one week, the snakes return to land for one to two weeks to digest their prey (Heatwole 1999, Shetty and Shine 2002, Brischoux and Bonnet 2008). During a long-term field study, we monitored snake populations on islets in the southwest lagoon (from north to south: Tenia, Mba, Signal, Larégnère, Amédée, Porc-Epic, Nouaré, Bayonnaise, Brosse; see Brischoux and Bonnet 2008 for a map of the study sites). Since 2002, we have captured by hand and uniquely marked (scale-clipped) 4714 individuals (2553 *L. saintgironsi* and 2161 *L. laticaudata*). Each snake was measured (snout-vent length-SVL,  $\pm 1$  cm), and weighed ( $\pm 1$  g). The two species overlap greatly in body sizes, with SVL ranges of 33.5 to 120.0 cm in *L. saintgironsi* and 38.0 to 137.0 cm in *L. laticaudata*. Further details on our procedures are available elsewhere (Brischoux et al. 2007b, Brischoux and Bonnet 2008).

We classified snakes smaller than 50 cm in SVL as young-of-the-year (based on growth rates from 4200 recaptures of marked individuals). From field observations (the smallest male engaged in courtship and the smallest female with vitellogenic follicles, as detected by palpation), we identified the minimal snout vent length at maturity as 75.5 cm (female) and 63.0 cm (male) for *L. saintgironsi*, and 88.5 cm (female) and 70.0 cm (male) for *L. laticaudata*. Snakes greater than 50 cm in length, but less than adult size, were classed as juveniles.

### Composition of the diet

The abdomen of each captured snake was palpated to detect the presence of a prey in the stomach; any items detected were gently pushed out the snake's mouth for identification and measurement. Sea-kraits feed mostly on non-spiny anguilliform fishes, easily regurgitated without risk of injury for the snake. Regurgitated prey were weighed, measured (total length and maximum midbody diameter) and later identified based on their dentition and other morphological traits (Böhlke et al. 1999, Smith 1999a, 1999b, Smith and McCosker 1999, Brischoux et al. 2007a). Previous analysis showed a low dietary overlap between the two sea krait species (Morisita-Horn similarity index of 0.15) and a strong contrast in their respective foraging habitats (hard bottoms for *L. saintgironsi* versus soft bottoms for *L. laticaudata*; Brischoux et al. 2007b). Despite a strong dietary divergence, the two taxa do overlap in terms of some of the prey species consumed, suggesting a broad similarity in foraging tactics (Brischoux et al. 2007b). We allocated each eel species to a habitat type (hard, soft, or hard-plus-soft substrates, Brischoux et al. 2007b) based on information in FishBase (Froese and Pauly 2006).

Although detailed data on the anguilliform fish community (e.g. species diversity and relative abundances) are lacking (Kulbicki 1997, Ineich et al. 2007), sea kraits feed on a large proportion (>50%) of the anguilliform species diversity in New Caledonia (50 species out of 93, M. Kulbicki, pers. comm.). Sampling these fishes via sea krait stomach contents provides a more comprehensive and

accurate assessment of anguilliform fish abundances and species diversity than does any other sampling method (Reed et al. 2002, Ineich et al. 2007, Séret et al. 2008). As a consequence, sampling anguilliform fish through sea kraits provides the best picture of this community to date.

Like any sampling method, reliance on snake stomach contents to quantify eel abundances is subject to bias. For example, the composition of a snake's diet may reflect preference for specific prey types, or greater ease of capture of some prey types, rather than comprising a random sample of the eels encountered. Indeed, some degree of prey selection must occur: for example, one eel species (*Echidna nebulosa*, a small- and medium-sized species) that we have often observed while diving on the reef flats (from where one third of prey are taken, Brischox et al. 2007b), has never been found in the snake's diet (n=1077 eels collected).

## Analyses

We performed richness estimates to test the effectiveness of our sampling of snake diets (Chao estimator, Colwell 2005). We calculated similarity indexes (Morisita-Horn index: Magurran 1988, 2004) to quantify dietary overlap between the three age classes (young-of-the-year, juveniles and adults) within each species. These analyses were performed using Estimates 7.5 (Colwell 2005). Other statistical tests (ANOVA, ANCOVA, linear regression, Contingency table, Fisher's PLSD as post-hoc tests) were performed with Statistica 7.1 (Statsoft 1984–2005).

## Results

### Morphology of prey

Body sizes and shapes differed between eels from hard-bottom versus soft-bottom habitats. Eels from hard coral tended to be much stouter-bodied than mud-burrowing species. Thus, ANOVA with habitat category (hard, hard plus soft, soft) as the factor, and prey dimensions as the dependent variables, showed that eels from hard-coral areas were shorter (prey length:  $F_{2,666} = 16.82$ ,  $p < 0.0001$ ) but thicker-bodied (prey diameter:  $F_{2,397} = 13.95$ ,  $p < 0.0001$ ) than eels from soft-bottom habitats; ubiquitous species (hard plus soft habitat) displaying an intermediate morphology (all posthoc tests  $p < 0.05$ ). Importantly for the critical issue of variation in body sizes within prey taxa, coefficients of variation of prey diameter averaged significantly lower for eel species from soft-bottom habitats (n = 3 prey species with suitably large sample sizes, mean  $\pm$  SD =  $0.15 \pm 0.02$ ) than for eel species from hard-coral habitats (n = 10 prey species, mean =  $0.26 \pm 0.07$ ;  $F_{1,11} = 5.76$ ,  $p < 0.04$ ).

### Interspecific and age-related differences in dietary diversity

We collected more prey items in *L. saintgironsi* (n = 655; 34 prey species) than in *L. laticaudata* (n = 365; 28 prey species), but the richness estimators in both species

plateaued after a sample size of 250 prey items, indicating that our sampling was adequate to quantify prey diversity (Colwell 2005). Moreover, the plateau was attained for all groups used for this analyses (the curves plateaued after 33 prey items for neonates, 80 for juveniles and 120 for adults in *L. laticaudata* and 20 for neonates, 80 for juveniles and 90 for adults in *L. saintgironsi*; Fig. 1). Beside indicating that our sampling was adequate to quantify prey diversity, such result suggests an increasing diet diversity with snake growth in both species (Fig. 1).

In *L. saintgironsi*, dietary composition changed little among age classes. Similarity indices were high for comparisons between young-of-the-year and juveniles (0.94), and between juveniles and adults (0.91). All individuals of this species tended to feed on the same prey species throughout their life. One moray-eel species (*Gymnothorax chilospilus*) comprised about half of all prey items found in this species; no other prey species comprised more than 9% of the diet (Table 1). Although detailed analysis suggests an increasing diet diversity with snake growth (2 eel species among 13 were eaten exclusively by young-of-the-year; 2 among 21 by the juveniles; and 13 among 30 by the adults), the prey taxa involved in this ontogenetic shift were minor components (<6%) of the overall diet.

In contrast, *L. laticaudata* age classes differed significantly in diet (similarity indices 0.70 between young-of-the-year and juveniles, and 0.24 between juveniles and adults). At least three prey species constituted >10% of the diet for each age class of predators (Table 1), with the identity of these dominant species shifting among predator age classes. For example, although young-of-the-year often fed on *Myrophis microchir* (38% of prey items), this species represented only 10% of the diet of juvenile snakes, and 1% for adults. Similarly, *Anarchias allardicei* represented 16% of the diet of juvenile snakes, but was never recorded in neonates or adults. Interestingly, the main prey species of *L. saintgironsi* (*G. chilospilus*) also occurred (albeit, much less commonly) in the diet of *L. laticaudata* (Table 1).

### Prey size

The most critical dimension of prey size for gape-limited predators such as snakes is likely to be maximum prey diameter. Accordingly, our analyses use this measure of prey size. As expected in gape-limited predators, larger snakes tended to feed on larger prey items (*L. saintgironsi*  $r^2 = 0.45$ , n = 536,  $p < 0.001$ ; *L. laticaudata*  $r^2 = 0.48$ , n = 228,  $p < 0.001$ ). This pattern is driven at least partly by gape-limitation, because the largest prey items (e.g. an eel >76 cm long) clearly could not be physically ingested by a neonate (<50 cm SVL) snake. Positive correlations between prey size and snake SVL were evident within as well as among prey species (e.g.  $r^2 = 0.14$ , n = 238,  $p < 0.001$  using *Gymnothorax chilospilus* for *L. saintgironsi*;  $r^2 = 0.67$ , n = 46,  $p < 0.001$  using *Conger* sp. for *L. laticaudata*). However, the ontogenetic increase in prey size was also achieved by the incorporation of larger prey species in the diet of larger snakes (Table 1, Fig. 2). In summary, larger snakes selected both larger fish (within each prey species) and larger prey species. The two snake species

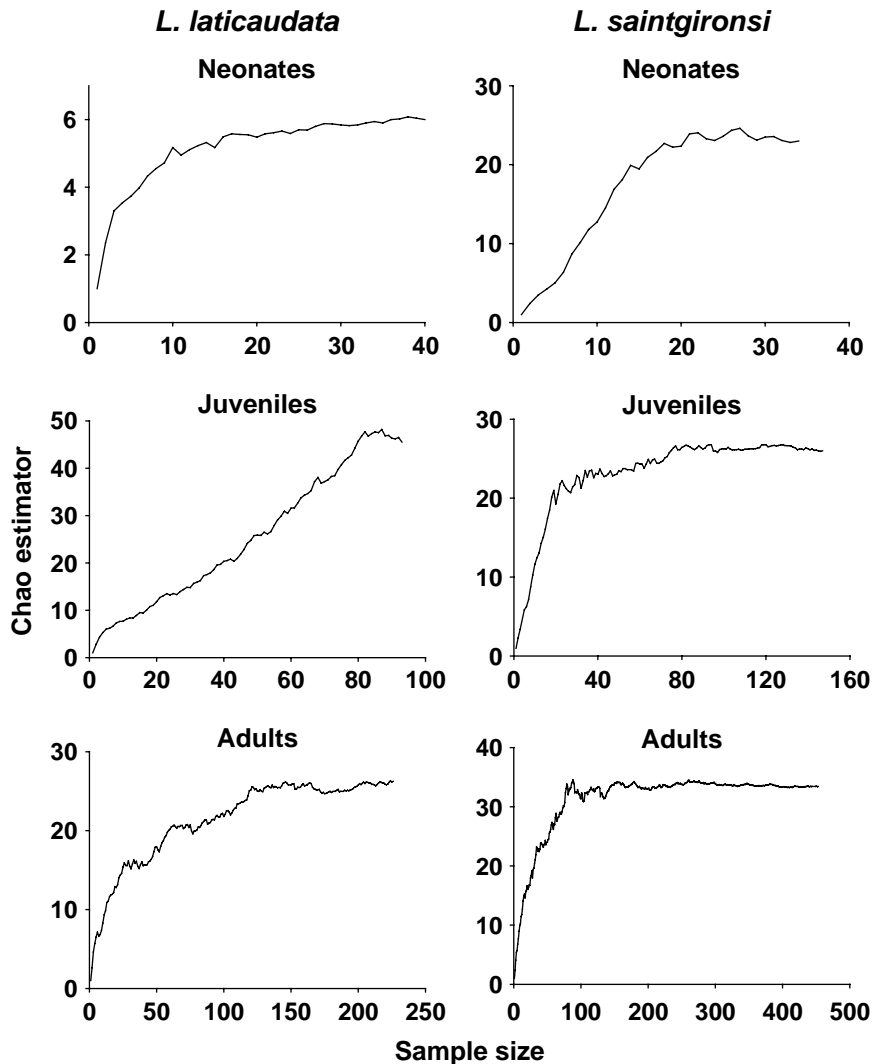


Figure 1. Adequacy of diet sampling, based on richness estimators for neonates, juveniles and adults of two species of sea kraits. All the curves reached a plateau, indicating that we adequately sampled the diet of each age class of snakes. Dietary diversity increases in older snakes; note that y- and x-axes differ in scale.

differed in the relative importance of these two mechanisms, however: *L. laticaudata* mostly took different (larger) prey species as they grew larger, whereas *L. saintgironi* tended to take larger individual prey items but of the same species as they consumed earlier in life (Table 1, Fig. 2). Nonetheless, very large *L. saintgironi* (>80 cm) tend also to shift to different (larger) prey species (Table 1, Fig. 2). However, none of these other species (n = 18) represented more than

8.5% in the diet of adult *L. saintgironi* whereas *G. chilospilus* (*L. saintgironi* main prey species) represented more than 44% of the diet of adult *L. saintgironi* (Table 1). The shift in prey size with increasing snake size was more pronounced in *L. saintgironi* than in *L. laticaudata* (ANCOVA with prey diameter as the dependent variable, snake species as the factor and snake SVL as the covariate: difference between the slopes  $F_{1,760} = 10.16$ ,  $p = 0.001$ ). In neonates, the length of

Table 1. Ontogenetic shifts in taxonomic composition of the diet in sea kraits (*Laticauda* spp.). The table shows the proportion of prey items (anguilliform fishes) of each species consumed by the neonates, juveniles and adults of two species of sea snakes. Prey species that comprised less than 10% of the diet are indicated without details (\*\* spp. =no. of species).

Species	Neonates		Juveniles		Adults	
<i>L. saintgironi</i>	<i>G. chilospilus</i>	48.5%	<i>G. chilospilus</i>	51.1%	<i>G. chilospilus</i>	44.4%
	12 sp.	51.5%	20 sp.	48.9%	29 sp.	55.6%
<i>L. laticaudata</i>	<i>M. microchir</i>	37.5%	<i>Conger</i> sp.	25.0%	<i>G. albimarginatus</i>	28.0%
	<i>Muraenichthys</i> . sp.	30.0%	<i>Muraenichthys</i> . sp.	16.4%	<i>Conger</i> sp.	23.4%
	<i>Conger</i> sp.	15.0%	<i>A. allardicei</i>	15.4%	<i>G. moluccensis</i>	13.5%
	<i>G. chilospilus</i>	10.0%	<i>G. albimarginatus</i>	14.5%		
			<i>M. microchir</i>	10.0%		
	2 spp.	7.5%	11 spp.	18.7%	19 spp.	35.1%

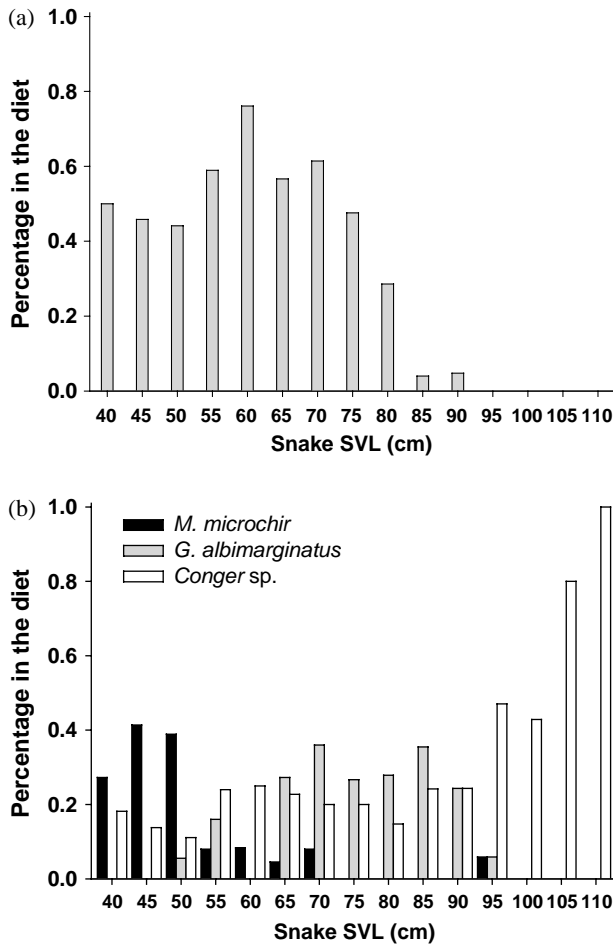


Figure 2. Size-related shifts in taxonomic composition of the diet in sea kraits (*Laticauda* spp.). The figure shows the proportion of the main ( $\geq 10\%$  of the total, Table 1) prey species eaten by 10 cm size classes of snakes, for each of the two *Laticauda* species: (a) in the hard-coral specialist *L. saintgironsi*, the single eel species *Gymnothorax chilospilus* spans a wide size range and hence is the main prey species for each age class. Note however that very large *L. saintgironsi* tend to shift to various other prey species ( $< 10\%$  of the adult diet, hence not displayed on the figure: see text and Table 1 for details); (b) in contrast, the soft-bottom eel species taken by *L. laticaudata* typically span a smaller size range and hence each is taken by a different size class of predator (*Myrophis microchir*, *G. albimarginatus* and *Conger* sp. are the main prey species of young-of-the-year, juvenile and adult snakes respectively).

the prey relative to the SVL of the snakes averaged  $54.0 \pm 1.6\%$  and  $41.1 \pm 0.7\%$  in *L. laticaudata* and *L. saintgironsi*, respectively; but these values were  $36.7 \pm 1.2\%$  and  $38.1 \pm 1.2\%$  in the adults, revealing that *L. saintgironsi* increased the size of its prey more steeply during growth. Overall, *L. saintgironsi* displayed a weak ontogenetic shift in prey composition combined with a steep ontogenetic increase in prey size, whereas *L. laticaudata* exhibited the reverse trend.

Reflecting these patterns, prey size (diameter) relative to snake body length showed clear divergences between snake species and between eels from different types of habitats. Similarly, soft-bottom eels (above) were thinner relative to the snakes that had consumed them (ANCOVA with prey diameter as dependent variable, eel habitat type as the

factor, snake SVL as covariate;  $F_{2,632} = 34.04$ ,  $p < 0.001$ ; posthoc tests have soft versus hard-bottom eels different at  $p < 0.05$ , Fig. 3). Interestingly, the correlation between prey size and predator size also was higher for soft-bottom eels (using absolute values of the residual scores from the general linear regression of prey size versus snake size as the measure of tightness of correlation:  $F_{2,633} = 4.57$ ,  $p < 0.015$ ; posthoc tests show soft-bottom eels significantly lower than either of the other habitat categories).

### Direction of prey ingestion

The degree of size-matching between anguilliform fishes and their crevices is lower in hard-coral areas than in eels from soft-bottom areas, because the former use existing (variably-sized) retreats whereas the latter excavate their own burrows. Thus, a snake seizing an eel in a hard-coral matrix may have more room to move, and be able to seize the eel at any part of its body. In contrast, a snake entering a burrow in soft-bottom areas will be likely to encounter (and thus, seize and swallow) the eel head-first. As predicted, *L. saintgironsi* seized and swallowed prey randomly with respect to direction (51% head first,  $n = 450$ ) whereas *L. laticaudata* swallowed head first most of the time (83% head first,  $n = 210$ ;  $\chi^2 = 62.8$ ,  $p < 0.001$ ).

### Discussion

Our field data document both strong similarities, and major divergences, in the trophic ecology of these two sympatric, congeneric sea snakes. Both feed almost entirely on anguilliform fishes, which they obtain by entering the crevices and burrows in which the eels live (Abrams et al. 1982, Ineich et al. 2007). Although the two snake taxa attain very similar body sizes, and return to the same islets

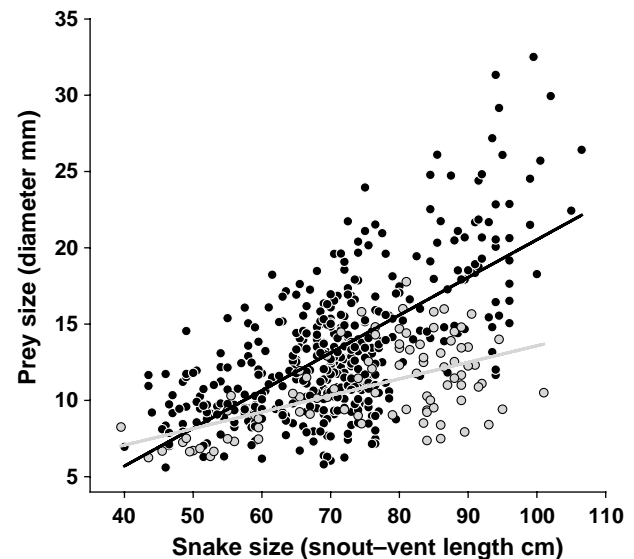


Figure 3. Relationship between snake size and prey diameter for prey taxa living in different types of habitat. Grey circles (grey regression line) for soft-bottom eels and black circles (black regression line) for hard-substrate eels. Soft-bottom eels were thinner relative to the snakes that had consumed them.

to digest their prey after foraging trips, they obtain their prey from different habitats within the Lagoon. Most of the eels taken by *L. saintgironsi* are obtained from among the interstices of hard coral, whereas many of the prey of *L. laticaudata* are taken from burrows in muddy (soft-bottom) areas (Brischoux et al. 2007b). That difference in foraging sites offers a plausible starting point for a sequence of events that ultimately cause divergence in dietary breadth between the two predator species.

Critically, eels from soft-bottom habitats are subject to biomechanical constraints on burrowing (these fishes must dig their own burrows, unlike the hard-coral eels) and constraints on maximal burrow diameter imposed by physical properties of the substrate (i.e. too large a burrow will collapse, Woolnough and Steele 2001). This situation generates important differences between burrowing eels and hard-coral eels. First, the burrowing eels tend to be relatively long and thin. Second, the range of body sizes within each species is smaller than in hard-coral taxa (perhaps reflecting specialization for particular substrate types). Third, eels are size-matched to their own burrows, so that any snake attempting to penetrate the burrow can be only marginally thicker than the eel inside. In combination, these factors generate a situation where *L. laticaudata* takes a wide range of prey species overall (although a narrow range within any given age class of snakes) and where prey size is highly correlated with predator size. In contrast, the eels taken by *L. saintgironsi* live within the hard-coral matrix, where crevices span an immense range and the eels can simply move to larger crevices as they grow larger. Size-matching of eel to crevice will be weaker, allowing a weaker correlation between prey size and predator size. More importantly, eel species in these habitats can span a wide size range (adjacent crevices are often of very different sizes, allowing easy movement between them), so that an ontogenetic increase in prey size within *L. saintgironsi* can be accomplished by simply taking larger individuals of the same eel species, rather than switching to different (larger) species. The divergence in the proportion of prey eaten head first between the two snake species supports the notion that the constraints imposed by the prey shape–prey habitat relationship are relaxed in hard substrates compared to soft bottoms.

Although we lack information on several aspects of the predator–prey relationship in this system (e.g. anti-predator tactics of eels, and the profitability of different prey types), the situation affords a robust comparison because the two predator–prey systems are similar in so many respects except for the habitat use of their prey. Under the hypothesis outlined above, the difference in dietary breadth between these two sympatric snake species ultimately is driven by habitat-imposed differences in constraints on body shape and size of the major prey taxa. Thus, the sea-snakes of the Neo-Caledonian Lagoon may provide an unusually clear example of the cascade of consequences from habitat structure through to prey morphology through to predator dietary diversity.

*Acknowledgements* – S. Lorient and M. De Crignis helped during fieldwork. R. Cambag protected the field camp against the rains. We also thank F. Devincq, C. Goiran and D. Ponton (Aquarium de Nouméa, DRN Province Sud, IRD). We thank the CNRS, the

Univ. François Rabelais and the Australian Research Council for funding. The study was carried out under permits no. 6024-179/DRN/ENV and no. 6024-3601/DRN/ENV.

## References

- Abrams, R. W. et al. 1982. Diurnal observations on the behavioral ecology of *Gymnothorax moringa* (Cuvier) and *Muraena miliaris* (Kaup) on a Caribbean coral reef. – *Coral Reefs* 1: 185–192.
- Amundsen, P.-A. et al. 1995. Experimental evidence of cannibalism and prey specialization in Arctic charr, *Salvelinus alpinus*. – *Environ. Biol. Fish.* 43: 285–293.
- Arnold, S. J. 1997. Foraging theory and prey size–predators size relations in snakes. – In: Seigel, R. A. and Collins, J. T. (eds), *Snakes. Ecology and behavior*. McGraw-Hill Inc, pp. 87–115.
- Beaudoin, C. P. et al. 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. – *Oecologia* 120: 386–396.
- Böhlke, E. B. et al. 1999. Muraenidae. – In: Carpenter, K. E. and Niem, V. H. (eds), *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific*. Vol. 3. pp. 1643–1657.
- Bolnick, D. I. et al. 2003. The ecology of individuals: incidence and implication of individual specialization. – *Am. Nat.* 161: 1–28.
- Brischoux, F. and Bonnet, X. 2008. Life history of sea kraits in New Caledonia. – *Mem. Mus. Nat. Hist. Nat.*, in press.
- Brischoux, F. et al. 2007a. A method to reconstruct anguilliform fishes from partially digested items. – *Mar. Biol.* 151: 1893–1897.
- Brischoux, F. et al. 2007b. Foraging ecology of sea kraits (*Laticauda* spp.) in the Neo-Caledonian lagoon. – *Mar. Ecol. Prog. Ser.* 350: 145–151.
- Camilleri, C. and Shine, R. 1990. Sexual dimorphism and dietary divergence: differences in trophic morphology between male and female snakes. – *Copeia* 1990: 649–658.
- Cogger, H. and Heatwole, H. 2006. *Laticauda frontalis* (de Vis, 1905) and *Laticauda saintgironsi* n. sp. from Vanuatu and New Caledonia (Serpentes: Elapidae: Laticaudinae) – a new lineage of sea kraits? – *Rec. Aust. Mus.* 58: 245–256.
- Colwell, R. K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Ver. 7.5. Persistent URL <[purl.oclc.org/estimates](http://purl.oclc.org/estimates)>.
- Froese, R. and Pauly, D. (eds) 2006. FishBase. World Wide Web electronic publication. <[www.fishbase.org](http://www.fishbase.org)> ver. 12/2006.
- Glodek, G. S. and Voris, H. K. 1982. Marine snake diets: prey composition, diversity and overlap. – *Copeia* 3: 661–666.
- Greene, C. H. 1986. Patterns of prey selection: implications of predator foraging tactics. – *Am. Nat.* 128: 824–839.
- Heatwole, H. 1999. Sea snakes. – *Aust. Nat. Hist. Ser.*, Univ. of New South Wales.
- Holbrook, S. J. and Schmitt, R. J. 1992. Causes and consequences of dietary specialization in surfperches: patch choice and intraspecific competition. – *Ecology* 73: 402–412.
- Ineich, I. and Laboute, P. 2002. Sea snakes of New Caledonia. – IRD Mus. Natl d'Hist. Nat. Editions, Collection Faune et flore tropicales, Paris.
- Ineich, I. et al. 2007. Anguilliform fishes and sea kraits: neglected predators in coral reef ecosystems. – *Mar. Biol.* 151: 793–802.
- Kulbicki, M. 1997. Bilan de 10 ans de recherche (1985–1995) par l'ORSTOM sur la structure des communautés des poissons lagonaires et récifaux en Nouvelle-Calédonie. – *Cybiurn* 21: 47–79.
- Magurran, A. E. 1988. Ecological diversity and its measurement. – Croom Helm.
- Magurran, A. E. 2004. Measuring biological diversity. – Blackwell.

- McDonald, R. A. 2002. Resource partitioning among British and Irish mustelids. – *J. Anim. Ecol.* 71: 185–200.
- Nyffeler, M. 1999. Prey selection of spiders in the field. – *J. Arachnol.* 27: 317–324.
- Peckarsky, B. L. 1982. Aquatic insect predator–prey relations. – *BioScience* 32: 261–266.
- Pierce, G. J. and Ollason, J. G. 1987. Eight reasons why optimal foraging theory is a complete waste of time. – *Oikos* 49: 111–117.
- Reed, R. N. et al. 2002. Sea kraits (*Squamata: Laticauda* spp.) as a useful bioassay for assessing local diversity of eels (*Muraenidae, Congridae*) in the western Pacific Ocean. – *Copeia* 2002: 1098–1101.
- Saint Girons, H. 1964. Notes sur l'écologie et la structure des populations des Laticaudinae (Serpentes: Hydrophiidae) en Nouvelle-Calédonie. – *Rev. Ecol. Terre Vie* 111: 185–214.
- Schoener, T. W. 1971. Theory of feeding strategies. – *Annu. Rev. Ecol. Syst.* 2: 369–404.
- Séret et al. 2008. First records of *Cirrimaxilla formosa* (Muraenidae) from New Caledonia, found in sea snake stomach contents. – *Cybio* 32:191–192.
- Shetty, S. and Shine, R. 2002. Activity patterns of yellow-lipped sea kraits (*Laticauda colubrina*) on a Fijian island. – *Copeia* 2002: 77–85.
- Shine, R. and Wall, M. 2007. Why is intraspecific variation in foraging biology more common in snakes than in lizards? – In: Reilly, S. M. et al. (eds), *Lizard ecology. Foraging modes in lizards*. Cambridge Univ. Press, pp. 173–208.
- Smith, D. G. 1999a. Myrocongridae: thin morays. – In: Carpenter, K. E. and Niem, V. H. (eds), *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 3*, pp. 1641–1642.
- Smith, D. G. 1999b. Congridae: Conger eels. – In Carpenter, K. E. and Niem, V. H. (eds), *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 3*, pp. 1680–1688.
- Smith, D. G. and McCosker, J. E. 1999. Ophichthidae: snake eels, worm eels. – In: Carpenter, K. E. and Niem, V. H. (eds), *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 3*, pp. 1662–1669.
- Steenhof, K. and Kochert, M. N. 1988. Dietary response of three raptor species to changing prey densities in a natural environment. – *J. Anim. Ecol.* 57: 37–48.
- Stephens, D. W. and Krebs, J. R. 1986. *Foraging theory*. – Princeton Univ. Press.
- Svanbäck, R. and Persson, L. 2004. Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. – *J. Anim. Ecol.* 73: 973–982.
- Tokeshi, M. 1999. *Species coexistence: ecological and evolutionary perspectives*. – Cambridge Univ. Press.
- Vézina, A. F. 1985. Empirical relationships between predator and prey size among terrestrial vertebrate predators. – *Oecologia* 67: 555–565.
- Vincent, S. E. et al. 2004. Sexual dimorphism in head shape and diet in the cottonmouth snake (*Agkistrodon piscivorus*). – *J. Zool.* 264: 53–59.
- Woolnough, A. P. and Steele, V. R. 2001. The paleoecology of the Vombatidae: did giant wombats burrow? – *Mamm. Rev.* 31: 33–45.