

A novel foraging mode in snakes: browsing by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae)

R. SHINE,† X. BONNET, M. J. ELPHICK and E. G. BARROTT

Biological Sciences A08, University of Sydney, New South Wales 2006, Australia

Summary

1. Ecologists often ascribe considerable importance to traits that are widespread within a specific lineage but rarely seen in other kinds of organisms. Unfortunately, such hypotheses cannot be tested robustly unless there is variation in expression of the trait within that lineage; such ‘exceptions to the rule’ provide opportunities to falsify predictions about putative functional correlates of the focal trait.

2. Research on snake foraging has emphasized species that feed infrequently and take large prey, often from ambush positions, but these characteristics do not apply to all snakes.

3. Movement patterns and feeding rates of free-ranging Turtle-Headed Sea Snakes *Emydocephalus annulatus* (Kreff 1869) were quantified in coral reefs of New Caledonia. These snakes forage by moving slowly (<2 m min⁻¹) but consistently across the substrate as they investigate crevices and burrows for fish nests. The snakes feed frequently (sometimes, several times per hour) on large numbers of very small (1 × 0.5 mm²) eggs. Snakes weighed more than one hundred thousand times as much as the prey items (eggs) they consumed, in contrast to high relative prey masses often reported for other snake species.

4. Field experiments in which snakes were exposed to a variety of stimuli indicate that these animals locate their prey by scent rather than visual cues.

5. The foraging mode of *Emydocephalus* (slow continuous movement, with frequent ingestion of small, immobile, defenceless food items) is more similar to that of herbivorous browsing mammals than to that of most macrostomate snakes.

6. In support of published hypotheses, *Emydocephalus* differ from most other snakes in traits predicted to be functionally associated with ingestion of large prey.

Key-words: Chemoreception, movements, New Caledonia, prey location, prey size.

Functional Ecology (2004) **18**, 16–24

Introduction

There is immense variation in the behaviours that predators use to locate and capture their prey. Foraging modes play a central role in interspecific ecological diversity, because they are intimately related to many other aspects of an organism’s biology. For example, research has suggested strong links between foraging tactics and attributes such as activity patterns (Brigham *et al.* 1999; Cooper *et al.* 2001), habitat use (Fedriani *et al.* 1999; Nakano *et al.* 1999), thermal and hydric relationships with the environment (Webb *et al.* 1995; Belliure & Carrascal 1996), social organization (Beauchamp 2002), body shape (Vitt & Congdon 1978; Barbosa & Moreno 1995), brain size (Iwaniuk & Nelson 2001), locomotor performance (Van Damme & Vanhooydonck 2001), digestive physiology (Hilton *et al.* 1999), metabolic

rate (Bedford & Christian 1998), the sensory modalities used for prey recognition (Cooper 1995; Linke *et al.* 2001), seasonal patterns of reproduction (Colli *et al.* 1997) and mortality (Willette *et al.* 1999), and life-history traits such as relative clutch mass, growth rates, ages at maturation and rates of female reproduction (Shine 1980; Huey & Pianka 1981; Simpson 1995; Webb & Shine 1998). Such correlates mean that foraging modes may predict vulnerability to anthropogenic hazards (Pekar 1999) and even to extinction in some lineages (Reed & Shine 2002).

The central role of foraging mode has stimulated many attempts at description and classification (see Perry 1999). Even for well-studied groups, however, detailed scientific attention has typically been directed towards a relatively small proportion of taxa, and in many cases the traits that have rendered such ‘model organisms’ amenable to study may also mean that they are not fully representative of foraging-mode diversity within the group as a whole. Snakes offer a good example

of this phenomenon. This group displays an array of remarkable adaptations related to patterns of food intake, and accordingly has attracted much analysis and speculation in terms of foraging modes (see review by Cundall & Greene 2000). Indeed, adaptations related to foraging have played a major role in the adaptive radiation of snakes (Gans 1961; Greene 1983a; Pough & Groves 1983; Mushinsky 1987; Cundall & Greene 2000). Most obviously, many modern snakes feed infrequently on prey items that are large relative to their own body size, and in this respect differ substantially from most modern lizards which instead focus on frequent ingestion of small prey (Greene 1983a; Pough & Groves 1983; Cundall & Greene 2000; Branch *et al.* 2002).

Reliance on infrequent large meals has been interpreted as a selective force for many of the distinctive traits of living snakes, including their morphology (e.g. venom delivery systems and constricting musculature; structural modifications to permit ingestion of large prey: Cundall 1987; Cundall & Greene 2000), physiology (low metabolic rates; organ down-regulation during periods between meals: Pough 1980; Secor & Nagy 1994; Secor & Diamond 1995, 1997), ecology (ontogenetic and sex-based shifts in dietary composition, long periods of inactivity: Mushinsky *et al.* 1982; Greene 1983b; Shine 1986) and behaviour (extreme selectivity with respect to prey type: Mushinsky 1987). Unfortunately, such hypotheses are easier to suggest than to test. The problem is a general one, applying to any trait (or correlated suite of traits) that is widespread (perhaps universal) within one lineage but rare in closely related lineages (e.g. flight in birds; blubber in cetaceans; placental nutrient transfer in eutherian mammals). Intuition suggests that the widespread trait is critically linked to other distinctive aspects of the biology of that particular lineage, but this hypothesis can be tested robustly only by comparing these animals with close relatives that do not display the trait in question. Ideally, we need to find species within the focal lineage that do not display the trait; then we can predict character states for other attributes that have been suggested to have some functional relationship with the critical trait.

The hypothesis that reliance on large infrequent meals has been a major selective force in the evolution of snakes is amenable to testing in exactly this way. Even within the macrostomate snakes (i.e. those that ingest large prey: Greene 1997), prey can be 'large' in a number of ways (e.g. mass *vs* body width), which impose selection on different attributes of the predators (e.g. subduing *vs* ingesting prey: Greene 1992). More importantly, many snake taxa rely upon relatively small prey items, such as the eggs or larvae of insects or amphibians (Greene 1983a, 1997). This trend has been recognized by many workers (and was dubbed 'ecological lizardisation' by Greene 1983a), but we have very little data on diets for most such snake species, and much less still on their foraging modes. Such information may enable direct tests of predictions based on the

putative central role of large, infrequent meals in the biology of macrostomate snakes.

Few published studies have quantified attributes of foraging mode in snakes such as distances travelled per unit time or feeding rates (Secor 1994) or the cues used to locate prey items (Shivik 1998). Indeed, a recent review (Cundall & Greene 2000, p. 302) pointed out that 'we know little about how most snakes find or catch prey except by inference and extrapolation from the behaviour of captive snakes'. For most sea snakes, we do not have even these data. One of the most exciting opportunities to investigate 'atypical' foraging modes in snakes involves specialization for small prey items by sea snake species that feed entirely on fish eggs. Specialist oophagy occurs in three species of sea snakes, and has been accompanied by profound modifications of morphology (Voris 1966; McCarthy 1987; Heatwole 1999). Because these animals appear to be extraordinarily divergent from 'typical' (macrostomate) snakes, we undertook a detailed study on foraging behaviour in one such species. More specifically, we quantified rates of movement and feeding, calculated relative prey sizes and examined the kinds of cues that these snakes use to locate their prey.

Materials and methods

STUDY SPECIES

The Turtle-Headed Sea Snake, *Emydocephalus annulatus* (Krefft 1869) is a shallow-water species found in reef habitats from New Caledonia to Australia (Cogger 1975; Ineich & Laboute 2002; Fig. 1). This medium-sized (to approx. 80 cm snout-vent length, SVL: Cogger 1975; Ineich & Laboute 2002) species feeds exclusively on the eggs of small fishes such as damselfish, blennies and gobies (Voris 1966; Guinea 1996; Ineich & Laboute 2002). The snakes are active only during daylight hours, and spend the night sleeping (M. Guinea, personal communication). We classed male snakes >45 cm SVL as adult based on sexually dimorphic rugose dorsal scalation, and arbitrarily used the same SVL cut-off for females. In New Caledonia, courtship and mating occur in winter (June-July); females give birth in the following autumn (May: Ineich & Laboute 2002; P. Borsa, personal communication; R. Shine, unpublished data).

STUDY AREA

Our study site was the southern end of the Baie des Citrons, a tourist beach in Noumea, New Caledonia (22°16' S, 166°26' E). We surveyed snake behaviour in a 60 × 60 m² area in water ranging from 0.8 to 5 m deep at high tide (0-4 m at low tide). Dives at other locations (Anse Vata, Isle Aux Canards, Porc-Epic) revealed very similar behaviour to that observed at the main study site. Water temperatures were 23-23.5 °C throughout our study in June-July (winter) and 27.5-28 °C during our study in December (summer).



Fig. 1. A juvenile Turtle-headed Sea Snake (*Emydocephalus annulatus*) foraging in shallow water on a coral reef in New Caledonia. Photograph by Pierre Laboute.

METHODS

Three observers snorkelled for 45–60 min twice per day during daylight hours over the periods 23 June to 4 July 2002 and 8–15 December 2002, except for a total of 4 days when storms precluded diving. We searched for foraging *Emydocephalus*, and followed animals for up to 10 min after they were located. At 60-s intervals we recorded (a) total distance moved, (b) straight-line displacement and (c) mean water depth traversed, over that period. Distances moved were determined by reference to features on the (highly heterogeneous) substrate; snakes were almost always very close to the ocean floor. We also recorded the number of times that the snake ascended to the surface to breathe, and the number of holes it investigated (i.e. into which it inserted its head) during that time. After 10 min (or sooner, if the snake began to move into an area of very shallow or very deep water where we could not follow), we captured the animal and returned it to the laboratory. Although our data thus are based mainly on foraging in relatively shallow water (0.5–3.5 m), extensive observations in deeper water reveal similar behaviours to those documented in our study (P. Laboute, personal communication).

From these behavioural data we estimated meander ratios (total distance travelled divided by straight-line distance: Secor 1994) and the number of feeding episodes. The latter variable could only be inferred not measured, because this activity frequently occurred with the snake's head deep inside a burrow or under a coral bommie. We classed a snake as 'feeding' if it remained immobile (i.e. total displacement of the midbody = 0 m) for at least 1 min. This immobility involved search time as well as actual prey consump-

tion; typically, such snakes stopped, began tongue-flicking more frequently and stayed within a small area (<1 m²) searching all available holes until they located the eggs. In some cases snakes remained immobile for much longer periods (up to 10 min) but these were classed as only single feeding events. Some of these cases may represent snakes that were inactive but not feeding, but in many instances we saw the snakes scraping fish-eggs from coral and ingesting them, as reported by Guinea (1996). Parental defence by damselfish against the snakes was common, but was never effective in repelling the marauding snake (Ineich & Laboute 2002).

All captured snakes (including some for which we did not obtain foraging data) were measured (SVL and total length), weighed and scored for sex (determined by tail shape, rugosity of dorsal scales and the sexually dimorphic rostral spine of adult males: Guinea 1996). Stomach contents were palpated by abdominal massage (preliminary dissections confirmed that palpation provided an accurate indication of the presence of food in the digestive tract), and collected in vials for later measurement under a Leitz MZ8 binocular microscope (40× with calibrated graticule). Subsamples of eggs were weighed in groups of 20. All snakes were scale-clipped before being returned to their place of capture; marked animals were often seen on later dives but no further data were taken on them, to avoid pseudoreplication.

To clarify the cues that *Emydocephalus* use to locate fish-eggs, we conducted experiments in which stimuli providing either visual or chemical (scent) cues from eggs were placed 5 cm from the snout of a free-ranging foraging snake. The eggs were obtained by palpating recently ingested (and hence undigested) eggs from

Table 1. Behaviours of free-ranging sea snakes, *Emydocephalus annulatus*, at Baie des Citrons in New Caledonia: sample sizes, with mean values and (in parentheses) associated standard errors per minute. Data are shown separately for studies conducted in winter (June–July) and summer (December)

	June–July 2002			December 2002	
	Adult males	Adult females	Juveniles	Adult males	Adult females
Number of snakes	20	8	10	8	6
Duration of observations (min)	7.50 (0.59)	9.13 (0.61)	9.50 (0.27)	8.50 (0.73)	6.33 (1.05)
Distance travelled (m) min ⁻¹					
straight-line	2.78 (0.49)	1.02 (0.33)	1.07 (0.20)	1.57 (0.12)	1.47 (0.74)
total	3.95 (0.62)	1.35 (0.42)	1.62 (0.24)	2.12 (0.23)	1.68 (0.74)
meander ratio	1.54 (0.07)	1.36 (0.11)	1.66 (0.15)	1.35 (0.10)	1.11 (0.05)
Holes checked min ⁻¹	3.08 (0.43)	2.17 (0.48)	4.00 (0.62)	2.21 (0.48)	1.68 (0.61)
Breaths min ⁻¹	0.04 (0.02)	0.00 (0.00)	0.03 (0.02)	0.04 (0.02)	0.08 (0.08)
Water depth (m)	1.17 (0.15)	1.45 (0.18)	0.94 (0.11)	1.95 (0.55)	2.01 (0.39)
'Feeding' episodes per 10 min	0	1.38 (0.32)	1.50 (0.31)	1.11 (0.22)	1.73 (0.63)

snakes captured while they were feeding. The eggs were placed in a double thickness of cotton cloth ('cheese-cloth') and washed in sea water; any digested eggs or fluids were thereby washed away, leaving only intact eggs. For the visual stimuli, we used tightly capped transparent plastic vials (10 mm diameter, 45 mm long) completely filled with eggs; the bright orange eggs were clearly visible. For the scent stimuli we used a double layer of cheesecloth wrapped around the eggs, forming a round bundle 15 mm in diameter. The porous cloth allowed scent but not intact eggs to disperse to the surrounding water. In both cases small lead fishing sinkers were added to make the stimulus sink, and a 2-m length of string allowed the experimenter to present the stimulus without disturbing the snake. Experiments testing scent and visual cues were run separately. Each snake was offered both an experimental stimulus and a control stimulus (identical vial or cheesecloth packages, but without eggs). Half the snakes received the control treatment first, and the other half was exposed to the experimental treatment first; analysis showed that order of presentation did not affect results. The investigator waited until a snake had its head in a crevice within the substrate; the stimulus was then gently lowered so that it rested beside the hole and was encountered as the snake withdrew its head. The number of tongue-flicks by the snake was scored over the following 30 s.

Results

We obtained data on movement patterns for a total of 38 snakes in winter (June–July) and 14 snakes in summer (December). Most observation periods lasted between 6 and 10 min (Table 1). Snakes were generally found in shallow water (<2 m deep), but ignored our presence even at distances of <1 m. Most animals did not surface to breathe during the observation period; breathing seems to occur about once every 20–30 min (Table 1). During such breaths the snakes swam rapidly to the surface, remaining there only a few seconds before diving back down. The rest of the time the animals

cruised slowly close to the substrate (a mosaic of coral rubble and live coral), poking their heads into crevices and holes (mean of about 2–3 holes min⁻¹: Table 1). Tongue-flicking was frequent, both when the snakes were in open water and when their heads were close to (or in contact with) the substrate.

No snakes <45 cm SVL were encountered in December, reflecting rapid growth of neonatal snakes born in May. To avoid spuriously 'significant' results from multiple tests on related variables (Cabin & Mitchell 2000), we conducted a multivariate ANOVA (MANOVA) on the combined data set, with season and sex as factors (excluding juveniles, because none was present in summer). The dependent variables are listed in Table 1. The MANOVA revealed that these traits did not differ significantly between the sexes (Pillai trace = 0.25, $F_{5,31} = 2.07$, $P = 0.10$) but differed between seasons (Pillai trace = 2.76, $F_{5,31} = 2.07$, $P < 0.04$). There was no statistically significant interaction between these factors (Pillai trace = 0.05, $F_{5,31} = 0.32$, $P = 0.90$). Inspection of individual ANOVAs revealed that the significant seasonal difference was due to trends for snakes to be in deeper water in summer than winter (Table 1; $F_{1,35} = 5.34$, $P < 0.03$) and to have higher meander ratios in winter ($F_{1,35} = 4.41$, $P < 0.05$). No other factors were significant in the individual ANOVAs.

To compare adult snakes to juvenile conspecifics within the winter sample, we conducted a one-factor MANOVA with age class as the factor. There was no significant difference between the two age groups in the behavioural traits that we measured (Pillai trace = 1.90, $F_{5,30} = 0.24$, $P = 0.12$). Hence, these analyses suggest that foraging activities and movement patterns of Turtle-Headed Sea Snakes do not vary significantly as a function of the sex or body size of the snake. Although the seasonal difference was statistically significant, it was relatively minor (Table 1).

Although all sex–age classes displayed similar meander ratios, breathing rates and numbers of holes investigated, adult males were never seen to feed during winter (Table 1) and rarely remained immobile (Fig. 2). Instead, they were actively engaged in mate-searching,

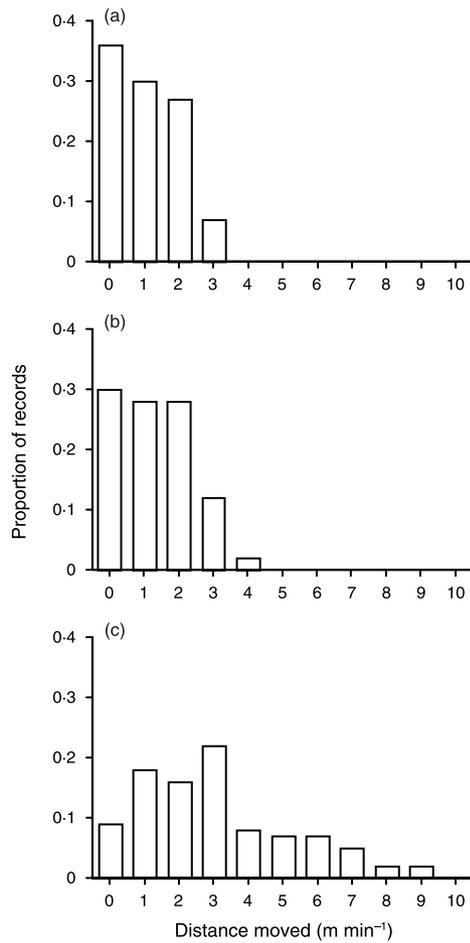


Fig. 2. Distances moved (m min^{-1}) by free-ranging sea snakes (*Emydocephalus annulatus*) in the Baie des Citrons, New Caledonia, in June–July 2002: overall frequency distributions, combining data for (a) 10 juveniles, (b) 8 adult females and (c) 20 adult males. See text for statistical analysis.

vigorously chasing and tongue-flicking any other snakes seen and courting any females. In contrast, most juveniles and adult females monitored at the same time spent at least 1 min during the observation period immobile and apparently, feeding (Table 1). Palpation of captured snakes revealed no prey items within the stomachs of any of the adult males collected in winter ($n = 38$ examined), but fish-eggs were regurgitated by many of the juveniles (9 of 12) and adult females (6 of 15) captured at this time ($\chi^2 = 32.05$, 2 df, $P < 0.0001$). The situation was very different in summer: no courtship was seen, and every snake that we palpated ($n = 26$ females, 13 males) contained thousands of freshly ingested fish-eggs. Thus, feeding frequencies varied seasonally in both sexes (females – $\chi^2 = 16.72$, 1 df, $P < 0.0001$; males – $\chi^2 = 36.62$, 1 df, $P < 0.0001$). The snakes with food in summer included 10 heavily gravid females and 11 snakes (6 males, 5 females) with extensive algal fouling and opaque eyes, clearly about to slough their skins.

In 14 of 16 palpated samples that we examined in detail, the eggs were oval in shape, white to orange in colour, and measured 0.7×0.4 – $0.8 \times 0.5 \text{ mm}^3$ in size.

In one other case the eggs were larger and more elongate ($1.3 \times 0.5 \text{ mm}^2$). Despite the narrow range in mean prey sizes, larger snakes contained smaller prey items (egg length: $n = 16$, $r = -0.54$, $P < 0.03$; egg width: $n = 16$, $r = -0.39$, $P = 0.14$). Some of the eggs were well developed with obvious eyespots in the embryos, but most displayed no overt sign of embryonic development. All these 15 samples were essentially undigested and, thus, may have been ingested shortly prior to the snake's capture; the remaining sample had eggs that had been broken down by digestion prior to our examination. All of the snakes that regurgitated prey contained thousands of eggs. This is likely to be a considerable underestimate, because many of these tiny items would escape detection during palpation. Mean individual egg mass averaged 0.00008 g (based on samples of 20 eggs each from 11 snakes), yielding a mean relative prey mass (individual prey item mass divided by snake mass) of 0.0000025 .

The trials of foraging cues provided clear-cut results. The two stimuli used to assess the role of vision (eggs inside a transparent plastic vial vs a vial containing sea water only) were placed beside the heads of 18 foraging snakes, but neither induced even a single tongue-flick from any of these animals. Presentations of the 'control' scent stimulus (cheesecloth bundle without eggs) to seven snakes similarly attracted almost no attention (1 tongue-flick total, so mean \pm SD per snake = 0.14 ± 0.38). In contrast, the same snakes exhibited 6.00 ± 4.24 tongue-flicks (range 2–15, paired $t = 3.98$, $P < 0.01$) to the cheesecloth bundle containing eggs (and, thus, providing scent cues).

Discussion

The foraging mode of *Emydocephalus* differs considerably from the 'classic' pattern reported for many macrostomate snakes: that is, infrequent ingestion of large (and sometimes, formidable) prey (e.g. Cundall & Greene 2000; Branch *et al.* 2002; Fearn 2002). *Emydocephalus* occupies a basal position in the hydrophiid radiation (Keogh *et al.* 1998; Rasmussen 2002) and all other hydrophiids except for two other egg-eaters (the congeneric *E. ijimae* and the closely related *Aipysurus eydouxii*) take much larger prey items than does *E. annulatus* (Voris & Voris 1983; Heatwole 1999). So do all of the terrestrial elapids thought to be close to the origin of this group (see Shine 1991). Thus, regardless of the details of its phylogenetic relationships, the situation in *Emydocephalus* must reflect a secondary reduction in prey size.

The closest parallels to *E. annulatus* in dietary composition involve other oophagous snake species. Specialist oophagy may have evolved only once within sea snakes, in the *Emydocephalus*–*Aipysurus* lineage (McCarthy 1987), but some terrestrial snake lineages have evolved to consume similarly small prey items. Many scolecophidian snakes (blindsnakes) specialize on the eggs and larvae of social insects (Webb & Shine

1993; Webb *et al.* 2000), and some colubrids feed extensively on the eggs of amphibians (Duellman & Trueb 1986; Warkentin 1995; Greene 1997). Snakes that specialize on large prey items will sometimes consume very small prey: for example, although Black Mambas (*Dendroaspis polylepis*) feed almost exclusively on endothermic vertebrates, there is one record of a 2-m specimen eating alate termites (Branch 1991; Branch *et al.* 1995). Thus, although adaptations to infrequent ingestion of large prey have undoubtedly played a seminal role in snake evolution, dietary reversals towards 'ecological lizardisation' (frequent ingestion of small prey) have occurred frequently. This is unsurprising, as many groups of animals display similar reversals in important adaptive traits (e.g. secondary flightlessness in birds; morphological simplification in secondarily parasitic species within many animal lineages).

The convergence towards a 'lizard' foraging mode is more pronounced for *Emydocephalus* than for scolecophidian snakes, which feed infrequently and take very large numbers of prey when they do so (Webb & Shine 1993; Webb *et al.* 2000). That is, blindsnakes consume small prey, but take them as large meals. In contrast, *E. annulatus* in our study took frequent meals that were small relative to the snake's body size (Table 1). Because *Emydocephalus* grows much larger than most blindsnakes, but consumes very small eggs, relative prey mass (RPM, the individual prey mass divided by snake mass) is lower in this taxon than in many (perhaps all) other snakes. We estimated mean RPM of approximately 0.000003, below the range of RPMs previously reported for lizards (e.g. 0.000004–0.28 in varanids: Losos & Greene 1988) or snakes (e.g. 0.11–0.82 in *Anilius*, 0.01–0.83 in *Cylindrophis*: Greene 1983a). Even terrestrial snakes that take small prey typically take larger items as well and thus, have higher RPMs than do *Emydocephalus*. For example, Seib (1984) reported ranges in RPM for three Mexican colubrids as 0.0007–0.16 (*Drymobius chloroticus*), 0.005–0.29 (*D. margaritifera*) and 0.005–0.55 (*Mastigodryas melanolomus*). The other unusual attribute of the diet of *E. annulatus* is that its prey (eggs) are immobile and, thus, no specific behaviours are needed to capture or subdue prey.

The foraging mode of *Emydocephalus* has strong analogies not only with lizards, but with other types of animals as well – especially herbivores. In feeding frequently on small immobile (and defenceless) prey items, the foraging mode of *Emydocephalus* is more similar to that of grazing or browsing mammals than to the kinds of foraging modes described for other snakes (e.g. ambush, slow searching or active pursuit). In turn, the kinds of conceptual models that have been developed for studying foraging in such animals (e.g. Spalinger & Hobbs 1992) might usefully be applied to these sea snakes.

As noted in the Introduction, data on 'exceptions' such as *Emydocephalus* can be used to test the validity and generality of hypotheses about the functional

consequences of reliance on large, infrequent meals by most snake species. If these hypotheses are valid, then *Emydocephalus*'s reliance on small prey should generate 'atypical' character states for other attributes functionally associated with prey size. Below, we review ideas and data relevant to several such hypotheses:

1. Organ down-regulation is an adaptation to long intervals between successive meals (Secor & Diamond 1995, 1997, 2000). We predict that *Emydocephalus* will not exhibit such down-regulation; this taxon would enable a powerful test of the hypothesis.
2. Large prey size results in gape-limitation, in turn generating size correlations between prey and predator (Arnold 1993). In support of this hypothesis, we saw a negative rather than positive correlation between predator size and prey size within *Emydocephalus*; we are not aware of any previous report of this situation in snakes. The larger egg sizes consumed by juvenile *Emydocephalus* presumably reflect their tendency to forage in shallower water than do the adults (Shine *et al.* 2003a), combined with the fact that snakes in shallow waters feed on the eggs of different fish species (Blennies rather than damselfish: Shine *et al.* 2003a).
3. Large prey size results in gape-limitation, in turn generating shifts in dietary composition between snakes of different body sizes (and, thus, sexes and ages) within a single population (Houston & Shine 1993; Luiselli & Angelici 1998). Apart from the minor shift in egg sizes noted above, we saw no dietary variation linked to sex or body size within *Emydocephalus*.
4. Large prey size results in gape-limitation, in turn favouring adaptations of morphology (flexible head conferring wide gape), physiology (venom) and/or behaviour (constriction) that facilitate the killing and ingestion of large prey (Cundall & Greene 2000). In keeping with this hypothesis, *Emydocephalus* does not display such features. Instead, the species of this genus exhibit evolutionary reductions in the ability to gape, as well as in the size of the fangs and venom gland and in the toxicity of their venom (Gopalakrishnakone & Kochva 1990; Guinea 1996; Ineich & Laboute 2002). Adaptations to scraping eggs from the substrate include enlargement of the supralabial scale (Guinea 1996) and possibly, modifications of throat musculature (McCarthy 1987).
5. Large prey size allows low feeding rates (Greene 1983a, 1992). Previous studies have noted that the proportion of snakes containing prey in their stomachs when collected is higher in *Emydocephalus* than in other sea snakes (Voris 1966; McCosker 1975; Heatwole *et al.* 1978). This was true in our study also, with prey found in 15 of 27 snakes (excluding adult males) examined in winter, and all of the 39 snakes that we palpated in summer. These proportions are much higher than in most other snake species (Martins *et al.* 2002).

6. Large prey size and low feeding rates permit long periods of inactivity (Fitch 1960; Secor 1994). The most extensive data sets on foraging mode in squamates come from studies on lizards, but again *Emydocephalus* is difficult to compare directly to these animals. For example, the main variables used to quantify foraging modes in lizards (e.g. moves per minute; mean proportion of time moving; Perry 1999) reflect the stop–start nature of terrestrial locomotion by these animals. In contrast, foraging *Emydocephalus* are almost constantly in motion, with currents and turbulence frequently moving them across the substrate even in the absence of active swimming (R. Shine, personal observation). Thus, the observed displacements do not necessarily reflect ‘voluntary’ moves as they would in a terrestrial species. Overall, *Emydocephalus* probably moves at a more consistent rate than do most foraging terrestrial reptiles (Fig. 2), and thus their percentage time moving during foraging activity (>80%: see Table 1) will also exceed that of most foraging lizards (see Perry 1999) and almost all other snakes (e.g. Heatwole *et al.* 1978; Greene 1983b; Slip & Shine 1988). Quantitative comparisons between foraging behaviours of *Emydocephalus* and those of other snakes are impeded by the scarcity of detailed behavioural studies on other taxa. Meander ratios averaged 2.1 (range 1–12.7) in foraging Sidewinders (Table 1 of Secor 1994), whereas our sea snakes typically moved more consistently in the same direction during a foraging bout (mean meander ratio 1.55, range 1–2.36: see Table 1). Presumably, this attribute will be affected in complex ways by habitat structure, snake foraging behaviour and by the distribution of prey. So will many other aspects of trophic biology, precluding any simple categorization of foraging behaviour (Perry 1999).
7. Reproduction entails cessation of feeding because foraging activities are incompatible with reproductive activities such as mate-searching by males, and additional basking by females (Aldridge & Brown 1995; Gregory *et al.* 1999). Again, the hypothesis is supported. Cessation of feeding by males during the mating season has been recorded for several taxa of terrestrial snakes including colubrids (Shine *et al.* 2003b), viperids (Bea *et al.* 1992; Madsen & Shine 1993; Aldridge & Brown 1995) and pythons (Madsen & Shine 2000). Both pregnancy and sloughing also interrupt feeding in many terrestrial snakes (Shine 1979; Gregory *et al.* 1999), but this was not the case in *Emydocephalus*. The lowered mobility of pregnant snakes (e.g. Seigel *et al.* 1987; Brodie 1989) and the impaired vision of snakes about to slough (Greene 1997) do not preclude feeding by *Emydocephalus* because foraging in these animals does not depend upon speed or visual acuity. Hence, the unusual foraging mode of *Emydocephalus* has implications for the energy costs of various activities: mate-searching males must forego feeding because these two activities are incompatible, whereas neither pregnancy nor sloughing prevent continued foraging.
8. Snakes that move about actively to feed have ‘faster’ life histories (quicker growth, earlier maturation) than snake species that capture prey from ambush (Reed & Shine 2002). As predicted, *Emydocephalus* show rapid growth and early maturation (at <12 months of age in males: Masunagai *et al.* 2003; R. Shine, unpublished data). Limited data on other sea snake taxa suggest that most delay maturation until at least the second year of life (Heatwole 1999).
9. A central dependency on chemoreception is one of the most distinctive attributes of snake biology (Greene 1992, 1997), and should be unrelated to prey size. That is, we do not expect *Emydocephalus* to diverge from other snakes in this respect. The frequent tongue-flicking of foraging *Emydocephalus*, and their intensive searching at specific sites, strongly suggest reliance on chemosensory cues to detect nearby egg masses (Ineich & Laboute 2002). Our experimental trials supported this inference; foraging snakes responded to scent but not to visual cues from prey items. Thus, the sensory systems that these snakes use to detect prey are similar to those used by their terrestrial relatives. The same system is important in varanoid lizards, and hence is likely to be an ancestral character for the entire radiation of snakes (Losos & Greene 1988). Dependence upon chemoreception in sea snake foraging suggests that debates on the origin of snakes (in terms of fossorial *vs* aquatic taxa: Lee & Caldwell 1998; Cundall & Greene 2000) do not challenge the central role of chemoreception in foraging throughout snake phylogeny.

In conclusion, foraging modes in snakes are more diverse than is often appreciated; and ‘atypical’ species such as *Emydocephalus annulatus* provide a broader perspective of foraging adaptations in snakes. Although previous workers have clearly been aware that not all ‘macrostomate’ snakes take large prey items, published discussions about general patterns in the trophic biology of snakes have tended to focus upon the remarkable suite of adaptations that allow some snakes to utilize very large prey. Our data support the idea that selective forces imposed by large prey items have played a major role in shaping the adaptive radiation of snakes, but a full understanding of foraging modes within this diverse clade of organisms can only come from much more detailed information on foraging behaviour in the field. For example, gape-limitation may be of trivial importance for many populations of snakes, because all available prey items are small enough for easy ingestion. Only empirical data can resolve this issue. Importantly, such studies should include not only the well-studied ‘model organisms’ that have been used to develop our current paradigms, but also species from other lineages, other habitats and other foraging modes. Our data on *Emydocephalus* show just how wide some of those divergences may be.

Acknowledgements

We thank Terri and Ben Shine for field assistance, and IRD Noumea (especially, Pierre Laboute) for logistical support. Pierre Laboute also kindly provided the photograph for Fig. 1. Funding was provided by the Australian Research Council.

References

- Aldridge, R.D. & Brown, W.S. (1995) Male reproductive cycle, age at maturity, and cost of reproduction in the timber rattlesnake (*Crotalus horridus*). *Journal of Herpetology* **29**, 399–407.
- Arnold, S.J. (1993) Foraging theory and prey-size–predator-size relations in snakes. *Snakes. Ecology and Behavior* (eds R.A. Seigel & J.T. Collins), pp. 87–116. McGraw-Hill, New York.
- Barbosa, A. & Moreno, E. (1995) Convergence in aerially feeding insectivorous birds. *Netherlands Journal of Zoology* **45**, 291–304.
- Bea, A., Brana, F., Baron, J.P. & Saint Girons, H. (1992) Régimes et cycles alimentaires des vipères européennes (Reptilia, Viperidae). *Année Biologique* **31**, 25–44.
- Beauchamp, G. (2002) Higher-level evolution of intraspecific flock-feeding in birds. *Behavioral Ecology and Sociobiology* **51**, 480–487.
- Bedford, G. & Christian, K. (1998) Standard metabolic rate and preferred body temperatures in some Australian pythons. *Australian Journal of Zoology* **46**, 317–328.
- Belliure, J. & Carrascal, L. (1996) Covariation of thermal biology and foraging mode in two Mediterranean lacertid lizards. *Ecology* **77**, 1163–1173.
- Branch, W.R. (1991) Unusual herpetological observations in the Kruger National Park. *African Herp News* **19**, 39–40.
- Branch, W.R., Haagner, G.V. & Shine, R. (1995) Is there an ontogenetic shift in mamba diet? Taxonomic confusion and dietary records for black and green mambas (*Dendroaspis*: Elapidae). *Herpetological Natural History* **3**, 171–178.
- Branch, W.R., Bauer, A.M. & Lamb, T. (2002) *Bitis caudalis* (horned adder). Prey size. *Herpetological Review* **33**, 137–138.
- Brigham, R., Gutsell, R., Wiacek, R. & Geiser, F. (1999) Foraging behaviour in relation to the lunar cycle by Australian owlet-nightjars *Aegotheles cristatus*. *Emu* **99**, 253–261.
- Brodie, E.D. III (1989) Behavioural modification as a means of reducing the cost of reproduction. *American Naturalist* **134**, 225–238.
- Cabin, R.J. & Mitchell, R.J. (2000) To Bonferroni or not to Bonferroni: when and how are the questions. *Bulletin of the Ecological Society of America* **81**, 246–248.
- Cogger, H.G. (1975) Sea snakes of Australia and New Guinea. *The Biology of Sea Snakes* (ed. W.A. Dunson), pp. 59–140. University Park Press, Baltimore.
- Colli, G., Peres, A. & Zatz, M. (1997) Foraging mode and reproductive seasonality in tropical lizards. *Journal of Herpetology* **31**, 490–499.
- Cooper, W.E.J. (1995) Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Animal Behaviour* **50**, 973–985.
- Cooper, W., Vitt, L., Caldwell, J. & Fox, S. (2001) Foraging modes of some American lizards: relationships among measurement variables and discreteness of modes. *Herpetologica* **57**, 65–76.
- Cundall, D. (1987) Functional morphology. *Snakes: Ecology and Evolutionary Biology* (eds R.A. Seigel, J.T. Collins & S.S. Novak), pp. 106–142. MacMillan, New York.
- Cundall, D. & Greene, H.W. (2000) Feeding in snakes. *Feeding. Form, Function and Evolution in Tetrapod Vertebrates* (ed. K.E. Schwenk), pp. 293–333. Academic Press, San Diego.
- Duellman, W.E. & Trueb, L. (1986) *Biology of Amphibians*. McGraw-Hill, New York.
- Fearn, S. (2002) *Morelia amethystina* (scrub python). *Diet. Herpetological Review* **33**, 58–59.
- Fedriani, J., Palomares, F. & Delibes, M. (1999) Niche relations among three sympatric Mediterranean carnivores. *Oecologia* **121**, 138–148.
- Fitch, H.S. (1960) Autecology of the copperhead. *University of Kansas Publications of the Museum of Natural History* **13**, 85–288.
- Gans, C. (1961) The feeding mechanism of snakes and its possible evolution. *American Zoologist* **1**, 217–227.
- Gopalakrishnakone, P. & Kochva, E. (1990) Venom glands and some associated muscles in sea snakes. *Journal of Morphology* **205**, 85–96.
- Greene, H.W. (1983a) Dietary correlates of the origin and radiation of snakes. *American Zoologist* **23**, 431–441.
- Greene, H.W. (1983b) Field studies of hunting behavior by bushmasters. *American Zoologist* **23**, 897.
- Greene, H.W. (1992) The ecological and behavioral context for pitviper evolution. *Biology of the Pitvipers* (eds J.A. Campbell & E.D.J. Brodie), pp. 107–117. Selva, Tyler.
- Greene, H.W. (1997) *Snakes. The Evolution of Mystery in Nature*. University of California Press, Berkeley.
- Gregory, P.T., Crampton, L.H. & Skebo, K.M. (1999) Conflicts and interactions among reproduction, thermoregulation and feeding in viviparous reptiles: are gravid snakes anorexic? *Journal of Zoology* **248**, 231–241.
- Guinea, M.L. (1996) Functions of the cephalic scales of the sea snake *Emydocephalus annulatus*. *Journal of Herpetology* **30**, 126–128.
- Heatwole, H.F. (1999) *Sea Snakes*. University of NSW Press, Sydney.
- Heatwole, H.F., Minton, S.A.J., Taylor, R. & Taylor, V. (1978) Underwater observations of sea snake behaviour. *Records of the Australian Museum* **31**, 737–761.
- Hilton, G., Houston, D., Barton, N., Furness, R. & Ruxton, G. (1999) Ecological constraints on digestive physiology in carnivorous and piscivorous birds. *Journal of Experimental Zoology* **283**, 365–376.
- Houston, D.L. & Shine, R. (1993) Sexual dimorphism and niche divergence: feeding habits of the arafura filesnake. *Journal of Animal Ecology* **62**, 737–749.
- Huey, R.B. & Pianka, E.R. (1981) Ecological consequences of foraging mode. *Ecology* **62**, 991–999.
- Ineich, I. & Laboute, P. (2002) *Sea Snakes of New Caledonia*. IRD Editions, Paris.
- Iwaniuk, A. & Nelson, J. (2001) A comparative analysis of relative brain size in waterfowl (Anseriformes). *Brain, Behavior and Evolution* **57**, 87–97.
- Keogh, J.S., Shine, R. & Donnellan, S.C. (1998) Phylogenetic relationships of terrestrial Australo-Papuan elapid snakes (subfamily Hydrophiinae) based on cytochrome *b* and 16S rRNA sequences. *Molecular Phylogeny and Evolution* **10**, 67–81.
- Lee, M.S.Y. & Caldwell, M.W. (1998) Anatomy and relationships of *Pachyrachis problematicus*, a primitive snake with hindlimbs. *Philosophical Transactions of the Royal Society of London B* **353**, 1521–1552.
- Linke, T., Platell, M. & Potter, I. (2001) Factors influencing the partitioning of food resources among six fish species in a large embayment with juxtaposing bare sand and seagrass habitats. *Journal of Experimental Marine Biology and Ecology* **266**, 193–217.
- Losos, J.B. & Greene, H.W. (1988) Ecological and evolutionary implications of diet in monitor lizards. *Biological Journal of the Linnean Society* **35**, 379–407.
- Luiselli, L. & Angelici, F.M. (1998) Sexual size dimorphism and natural history traits are correlated with intersexual dietary divergence in royal pythons (*Python regius*) from the rainforests of southeastern Nigeria. *Italian Journal of Zoology* **65**, 183–185.

- Madsen, T. & Shine, R. (1993) Costs of reproduction in a population of European adders. *Oecologia* **94**, 488–495.
- Madsen, T. & Shine, R. (2000) Energy versus risk: costs of reproduction in free-ranging pythons in tropical Australia. *Austral Ecology* **25**, 670–675.
- Martins, M., Marques, O.A.V. & Sazima, I. (2002) Ecological and phylogenetic correlates of feeding habits in neotropical pitvipers of the genus *Bothrops*. *Biology of the Vipers* (eds G.W. Shuett, M. Höggren, M.E. Douglas & H.W. Greene), pp. 307–328. Eagle Mountain Publishing, Utah.
- Masunagai, G., Matsuura, R., Yoshino, T. & Ota, H. (2003) Reproductive biology of the viviparous sea snake *Emydocephalus ljimae*. Reptilia: Hydrophiidae) under a seasonal environment in the Northern Hemisphere. *Herpetological Journal* (in press).
- McCarthy, C.J. (1987) Adaptations of sea snakes that eat fish eggs; with a note on the throat musculature of *Aipysurus eydouxii* (Gray 1849). *Journal of Natural History* **21**, 1119–1128.
- McCosker, J.E. (1975) Feeding behavior of Indo-Australian Hydrophiidae. *The Biology of Sea Snakes* (ed. W.A. Dunson), pp. 217–232. University Park Press, Baltimore.
- Mushinsky, H.R. (1987) Foraging ecology. *Snakes: Ecology and Evolutionary Biology* (eds R.A. Seigel, J.T. Collins & S.S. Novak), pp. 302–334. MacMillan, New York.
- Mushinsky, H.R., Hebrard, J.J. & Vodopich, D.S. (1982) Ontogeny of water snake foraging ecology. *Ecology* **63**, 1624–1629.
- Nakano, S., Fausch, K. & Kitano, S. (1999) Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. *Journal of Animal Ecology* **68**, 1079–1092.
- Pekar, S. (1999) Foraging mode: a factor affecting the susceptibility of spiders (Araneae) to insecticide applications. *Pesticide Science* **55**, 1077–1082.
- Perry, G. (1999) The evolution of search modes: ecological versus phylogenetic perspectives. *American Naturalist* **153**, 98–109.
- Pough, F.H. (1980) The advantages of ectothermy for tetrapods. *American Naturalist* **115**, 92–112.
- Pough, F.H. & Groves, J.D. (1983) Specialization in the body form and food habits of snakes. *American Zoologist* **23**, 443–454.
- Rasmussen, A.R. (2002) Phylogenetic analysis of the 'true' aquatic elapid snakes Hydrophiinae (sensu Smith *et al.* 1977) indicates two independent radiations into water. *Steenstrupia* **27**, 47–63.
- Reed, R.N. & Shine, R. (2002) Lying in wait for extinction? Ecological correlates of conservation status among Australian elapid snakes. *Conservation Biology* **16**, 451–461.
- Secor, S.M. (1994) Ecological significance of movements and activity range for the sidewinder, *Crotalus cerastes*. *Copeia* **1994**, 631–645.
- Secor, S.M. & Diamond, J. (1995) Adaptive responses to feeding in Burmese pythons: pay before pumping. *Journal of Experimental Biology* **198**, 1315–1325.
- Secor, S.M. & Diamond, J. (1997) Effects of meal size on postprandial responses in juvenile Burmese pythons (*Python molurus*). *American Journal of Physiology* **272**, R902–R912.
- Secor, S.M. & Diamond, J. (2000) Evolution of regulatory responses to feeding in snakes. *Physiological and Biochemical Zoology* **73**, 123–141.
- Secor, S.M. & Nagy, K.A. (1994) Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* **75**, 1600–1614.
- Seib, R.L. (1984) Prey use in three syntopic neotropical racers. *Journal of Herpetology* **18**, 412–420.
- Seigel, R.A., Huggins, M.M. & Ford, N.B. (1987) Reduction in locomotor ability as a cost of reproduction in snakes. *Oecologia* **73**, 481–465.
- Shine, R. (1979) Activity patterns in Australian elapid snakes (Squamata: Serpentes: Elapidae). *Herpetologica* **35**, 1–11.
- Shine, R. (1980) Ecology of the Australian death adder, *Acanthophis antarcticus* (Elapidae): evidence for convergence with the Viperidae. *Herpetologica* **36**, 281–289.
- Shine, R. (1986) Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. *Oecologia* **69**, 260–267.
- Shine, R. (1991) *Australian Snakes. A Natural History*. Reed Books, Sydney.
- Shine, R., Shine, T. & Shine, B. (2003a) Intraspecific habitat partitioning by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae): the effects of sex, body size, and color pattern. *Biological Journal of the Linnean Society* **80**, 1–10.
- Shine, R., Phillips, B., Wayne, H. & Mason, R.T. (2003b) Behavioral shifts associated with reproduction in garter snakes. *Behavioral Ecology* **14**, 251–256.
- Shivik, J.A. (1998) Brown tree snake response to visual and olfactory cues. *Journal of Wildlife Management* **62**, 105–111.
- Simpson, M. (1995) Covariation of spider egg and clutch size – the influence of foraging and parental care. *Ecology* **76**, 795–800.
- Slip, D.J. & Shine, R. (1988) Feeding habits of the diamond python, *Morelia s. spilota*: ambush predation by a boid snake. *Journal of Herpetology* **22**, 323–330.
- Spalinger, D.E. & Hobbs, N.T. (1992) Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist* **140**, 325–347.
- Van Damme, R. & Vanhoooydonck, B. (2001) Origins of interspecific variation in lizard sprint capacity. *Functional Ecology* **15**, 186–202.
- Vitt, L.J. & Congdon, J.D. (1978) Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *American Naturalist* **112**, 595–608.
- Voris, H.K. (1966) Fish eggs as the apparent sole food item for a genus of sea snake, *Emydocephalus* (Krefft). *Ecology* **47**, 152–154.
- Voris, H.K. & Voris, H.H. (1983) Feeding strategies in marine snakes: an analysis of evolutionary, morphological, behavioral and ecological relationships. *American Zoologist* **23**, 411–425.
- Warkentin, K.M. (1995) Adaptive plasticity in hatching age – a response to predation risk trade-offs. *Proceedings of the National Academy of Sciences of the United States of America* **92**, 3507–3510.
- Webb, J.K. & Shine, R. (1993) Dietary habits of Australian blindsnakes. *Copeia* **1993**, 762–770.
- Webb, J.K. & Shine, R. (1998) Ecological characteristics of a threatened snake species, *Hoplocephalus bungaroides* (Serpentes, Elapidae). *Animal Conservation* **1**, 185–193.
- Webb, P., Speakman, J. & Racey, P. (1995) Evaporative water-loss in two sympatric species of vespertilionid bat, *Plecotus auritus* and *Myotis daubentoni* – relation to foraging mode and implications for roost site selection. *Journal of Zoology (London)* **235**, 269–278.
- Webb, J.K., Shine, R., Branch, W.R. & Harlow, P.S. (2000) Life history strategies in basal snakes: reproduction and dietary habits of the African threadsnake, *Leptotyphlops scutifrons* (Serpentes, Leptotyphlopidae). *Journal of Zoology (London)* **250**, 321–327.
- Willette, T., Cooney, R. & Hyer, K. (1999) Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 364–376.

Received 31 March 2003; revised 14 August 2003; accepted 26 August 2003