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Antipredator Tactics of Amphibious Sea-Snakes (Serpentes, Laticaudidae)

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Abstract

Because the antipredator behavior that an animal displays depends upon the context in which it encounters the predator, apparent interspecific differences in antipredator tactics may result from ecological rather than behavioral differences among taxa. We approached 127 free-ranging laticaudid sea-snakes on small islands in Noumea Lagoon, New Caledonia, prodded the animals midbody, and recorded their responses. One species (*Laticauda colubrina*) usually remained immobile (relying on crypsis) whereas another (*L. laticaudata*) generally fled. However, multivariate analysis shows that the two species actually responded in very similar ways to any given stimulus; the species differed overall because *colubrina* was generally encountered on land during the day whereas *laticaudata* was more often encountered in the ocean at night. Thus, apparent interspecific differences in antipredator responses were secondary consequences of interspecific differences in the times and places that predators were encountered. Snakes were more likely to flee rather than remain immobile when rapid locomotion was possible (i.e. juveniles rather than adults; in water rather than on land) and pursuit by a predator was difficult (i.e. at night rather than during the day). These patterns suggest that snakes adjust their antipredator tactics in ways that maximize the chances of surviving the encounter, although the remarkable docility of these highly venomous snakes remains puzzling.

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Introduction

Although interspecific differences in behavior are widespread, the factors that generate this diversity are obscure for most kinds of behaviors in most kinds of organisms. Two primary challenges for ethologists are (1) to evaluate the degree to which this interspecific diversity in behavioral responses is generated by genes that code for specific behaviors, as opposed to being consequences of environmental differences among species; and (2) to clarify the

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adaptive significance of intraspecific plasticity in such responses. For study systems that can be taken into the laboratory, sophisticated approaches such as quantitative genetics and carefully controlled experiments (e.g. Arnold & Bennett 1984; Brodie 1989, 1992; Hopper 2001; Smith & Belk 2001) can provide unequivocal answers to these questions. For many systems, however, laboratory experimentation is never likely to be feasible. This is especially true for complex and flexible behaviors, such as antipredator responses: even brief periods in captivity can modify antipredator behavior in some species (Fitch 1975; Greene 1988). Also, it is difficult to simulate the complexity of natural environments under laboratory conditions, and thus important cues may be inadvertently eliminated from the experimental design. Field studies are an essential first step to identify correlates of (and hence, potentially, influences on) antipredator behavior (Gibbons & Dorcas 2002).

If we are restricted to field studies, how can we determine whether an observed difference in antipredator responses between two taxa is due to genetically determined divergence in the behavior *per se* (i.e. under the same conditions, species X responds differently from species Y) rather than interspecific differences in the ecological context within which the taxa are encountered (i.e. species X and Y have identical responses to the same stimuli, and behave differently because they encounter predators in different situations)? One solution to these problems is to study sympatric species in the field, and to record antipredator responses to standardized stimuli while at the same time recording multiple aspects of potentially relevant factors (such as the animal's species, sex and size; and the habitat, time of day, etc.). Multivariate analyses can then consider the influence of each of these factors simultaneously, and clarify interspecific differences after removing the confounding influences of other variables.

A second ambiguity in published studies concerns plasticity in antipredator responses within a single species. Intuition suggests that animals will modify their responses in the light of the effectiveness of alternative tactics, and considerable data support this inference (Lima & Dill 1990). For example, cold reptiles tend to rely on crypsis or display, whereas hotter reptiles (that are thereby more capable of rapid locomotion) tend to rely on flight instead (e.g. Passek & Gillingham 1997; Shine et al. 2000). To robustly test the hypothesis that animals use the most effective antipredator tactic available to them in a given situation, we need study systems in which clear discontinuities in the putative determinants of responses allow clear, unambiguous *a priori* predictions about behavior.

We have worked with a system that allows us to examine both of the questions outlined above. In many Pacific islands, laticaudid sea-snakes occur in abundance and frequently, in sympatry. These snakes forage in the ocean but return to land to digest their prey, slough their skins, court, mate and lay eggs (Heatwole & Guinea 1993; Heatwole 1999). Importantly, the snakes can move about threefold faster in water than on land (Shine & Shetty 2001; Shine et al., unpubl. data), generating a strong habitat discontinuity in the animal's ability to flee rapidly from predators. We made the following *a priori* predictions because:

(1) the snakes can move much faster in water than on land, animals on land would frequently rely on crypsis whereas aquatic snakes would flee;

(2) low light levels at night facilitate evasion of predators (especially in species with banded patterns that confuse predators with flicker-fusion: Jackson et al. 1976), snakes at night would flee whereas those encountered during the day would be more likely to rely on crypsis;

(3) small snakes swim and crawl faster than larger conspecifics (in terms of body lengths/s: Shine & Shetty 2001), small snakes should rely more on flight than on crypsis; and

(4) the two species within our study area (and the sexes within these species) show relatively similar locomotor speeds (see below), we do not expect to see strong interspecific or sex-based divergence in antipredator responses.

Methods

Study Species

Sea-snakes of the family Laticaudidae ('sea-kraits': Heatwole 1999) are brightly banded amphibious venomous snakes that are widely distributed through the Pacific Ocean. Two species of laticaudids are abundant on islands in the Noumea Lagoon of New Caledonia (22°16′S, 166°26′E). One of these taxa (currently referred to the wide-ranging *Laticauda colubrina*, but soon to be elevated to separate species status: H. G. Cogger et al., in prep.) has brown to orange bands between its black bands; it is relatively heavy-bodied with marked sexual size dimorphism (for our sample of New Caledonian animals, maxima of 80 cm snout-vent length (SVL), 190 g for males; 107 cm, 500 g for females). The other taxon, *L. laticaudata* is a more elongate snake with brilliant blue between the black bands. Sexual dimorphism is less marked in this taxon (for our sample of New Caledonian animals, maxima of 96 cm SVL, 330 g for males; 155 cm, 430 g for females). Both species feed exclusively on fishes (primarily eels) but return to small islands for non-foraging activities. Radiotelemetric monitoring of a Fijian population of *L. colubrina* showed that the animals spent about equal time on land as in the water, moving between the two habitat types every 10 d or so (Shetty & Shine 2002).

Although the ecology of New Caledonian laticaudids remains poorly known (Saint Girons 1964), *L. colubrina* has been reported to use terrestrial habitats (including those relatively far from water) to a greater degree than does *L. laticaudata* (Greer 1997). Trials in which snakes were timed along raceways show that both taxa were much faster in water than on land (*colubrina*, mean speeds of 1.00 vs. 0.27 body lengths/s; *laticaudata*, 0.80 vs. 0.29 body lengths/s; for absolute speeds, *colubrina*, 0.77 vs. 0.21 m/s; *laticaudata*, 0.61 vs. 0.21 m/s: Shine et al., unpubl. data). Small snakes were slower than larger animals in absolute terms, but much faster in terms of body lengths/s (Shine & Shetty 2001); the latter measure is likely to be more important than the former for evading predators (Van Damme & Van Doren 1999).

The geographic range of laticaudids spans a diverse array of small isolated island groups, which differ substantially in the abundance and composition of potential predators for these snakes. Aquatic predators in New Caledonia include tiger sharks (P. Laboute, pers. comm.), but these islands lack sea eagles that have been reported to prey on laticaudids (both on land and in the water) in other parts of their range (Stuebing 1988; Shetty & Prasad 1996). Large crabs and fishes may sometimes take juvenile laticaudids (Guinea 1986).

We used humans as the predatory stimulus in our study, as has been the case in most other field-based research on snake antipredator tactics. People are the major present-day terrestrial predator on laticaudids in New Caledonia (Saint Girons 1964), but have been present in the islands so briefly (<4000 yr: Bauer & Sadlier 2000) that they are unlikely to have been a selective force on the snakes' antipredator behavior. There is no commercial harvest or domestic utilization of sea-snakes in New Caledonia, so mortality due to human attack is episodic and probably generally rare. However, snakes tend to respond to a wide range of potentially threatening stimuli in similar ways, with the human hand eliciting the same kinds of responses as a realistic model of the predator (Scudder & Chiszar 1977; Herzog et al. 1989; Shine et al. 2000). Using humans as 'predators' also overcomes major ethical issues in the use of live natural predator species.

We gathered data on free-ranging laticaudids on two small islands (Signal and Porc-Epic) in Noumea Lagoon over the period 17–21 January 2002. Preliminary analysis revealed very similar behaviors for snakes on the two islands, and thus data were pooled for analysis. We searched for snakes that were potentially visible to a predator (i.e. with the body partially or wholly exposed, rather than hidden beneath rocks or coral). The observer walked directly towards the snake, and then prodded the snake's midbody with a fingertip three times at 1-s intervals. We then scored the animal's response over the following 5 s. Following scoring of the response, the snake was collected so that we could record its species, sex (determined by eversion of hemipenes), and SVL. Ambient (air and water) temperatures and body temperature of the snake were recorded with an electronic thermometer (Comark KM45, Comark Ltd, Herts, UK). Dusk falls rapidly in this tropical area, with a sudden shift in light intensity, so records were also divided into diurnal and nocturnal readings (before or after 19:00 hours). After scoring, snakes were retained in cloth bags to ensure that no animal was recorded more than once; all snakes were released unhurt <12 h after collection.

Results

We obtained data on attributes (species, sexes, sizes, temperatures) of 127 snakes (39 *colubrina* and 88 *laticaudata*), on the times and places they were encountered, and on their responses to us. Ambient temperatures and body temperatures of snakes remained within a narrow range (24.9–29.5°C) and did not differ between land and water (for ambient temperatures, $\bar{x} = 26.7$ vs. 27.0°C; $F_{1,125} = 0.65$, $p = 0.42$; for body temperatures of snakes, $\bar{x} = 27.3$ vs. 27.4°C; $F_{1,125} = 0.11$, $p = 0.73$). The analysis below is divided into two sections. First, we examine how a snake's species, sex and body size influenced where and when it was found, because any biases in these respects might affect the animals' antipredator responses. We then consider the snakes' behavior.

To identify non-random associations between snake attributes and environmental factors, we used multiple logistic regression with species, sex and SVL as independent variables. Whether the snake was found by night or day was affected by species (likelihood ratio tests from logistic regression, $\chi^2 = 13.96$, 1 df, $p = 0.0002$; 87% of *colubrina* records were from daylight hours vs. 48% for *laticaudata*) but not by either the animal's sex ($\chi^2 = 1.93$, 1 df, $p = 0.16$) or its body size ($\chi^2 = 1.19$, 1 df, $p = 0.28$). Very similar results were obtained for the regression on whether the snake was found in water vs. on land. The two laticaudid species differed in this respect ($\chi^2 = 25.15$, 1 df, $p = 0.0001$; 95% of *colubrina* vs. 53% of *laticaudata* were encountered on land), but a snake's sex ($\chi^2 = 0.74$, 1 df, $p = 0.39$) and SVL did not affect its probability of being located in a terrestrial vs. aquatic habitat ($\chi^2 = 3.06$, 1 df, $p = 0.08$). In summary, *L. colubrina* were often found during the day and on land, whereas *L. laticaudata* were mostly found at night and in the water. However, neither sex nor body size had significant effects on the animal's location.

No snake responded overtly to our approach until touched, nor did they display or attempt to bite. We divided responses into two categories: snakes that remained still (reliance on crypsis) vs. those that attempted to escape. We carried out two separate analyses on these data. First, we conducted univariate tests to look at how responses differed according to snake attributes, time and habitat. This analysis simply asks if responses differed among various groups of animals, without allowing for covariation among the independent variables. We then conducted a multivariate analysis, including all of the measured variables, to see if any of the 'significant' differences revealed by univariate analyses are secondary consequences of differences in times and places of encounter among animals. Such indirect effects should disappear in the multivariate analysis.

For consistency, we used logistic regression for all of these tests. The proportion of snakes that fled from our approach (rather than remaining still) differed strongly between the two species (49% of *colubrina* fled vs. 84% of *laticaudata*; $\chi^2 = 16.41$, 1 df, $p = 0.0001$). However, the proportion of snakes that fled did not differ between sexes within each species (overall, 61% of females fled vs. 78% of males; *colubrina*, $\chi^2 = 1.30$, 1 df, $p = 0.25$; *laticaudata*, $\chi^2 = 0.01$, 1 df, $p = 0.92$). Body length influenced antipredator responses, with smaller snakes more likely to flee (*colubrina*, $\chi^2 = 6.81$, 1 df, $p = 0.009$; *laticaudata*, $\chi^2 = 4.99$, 1 df, $p = 0.003$). Snakes were more likely to flee at night than by day (overall, 98 vs. 57% of snakes; for *colubrina*, $\chi^2 = 7.97$, 1 df, $p = 0.005$; *laticaudata*, $\chi^2 = 15.51$, 1 df, $p = 0.0001$). *Laticauda laticaudata* in water were more likely to flee than were those on land (93 vs. 77%, $\chi^2 = 4.51$, 1 df, $p = 0.03$). *Laticauda colubrina* showed the same trend, but because of small sample sizes (only two snakes of this species were found in the water), the pattern did not attain statistical significance (100 vs. 46%; $\chi^2 = 2.99$, 1 df, $p = 0.08$). Figure 1 shows these patterns graphically.

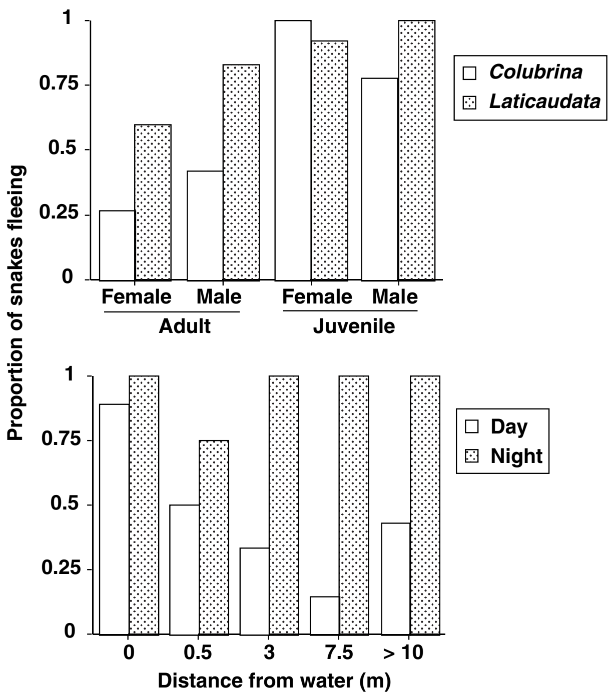

Fig. 1: Antipredator responses of two species of laticaudid sea-snakes in New Caledonia. The upper graph shows the proportion of snakes that fled from the stimulus as a function of the snake's species, sex and body size (all snakes < 70 cm snout-vent length were defined as juveniles, and all individuals greater than this size as adults). The lower graph combines data for snakes of different species, sizes and sexes to examine the effects of time (day vs. night) and distance from water as determinants of whether or not a snake fled from the stimulus. See text for statistical analyses of these data

Thus, the univariate analyses suggest that whether or not a snake fled from our approach was affected by a host of factors including its species, body size, location (land vs. water) and time (day vs. night). However, these factors are not orthogonal, because biases in snake activity times and habitat selection generated correlations between snake attributes (especially, species) and other traits (see above). We can control for these patterns of covariation by running a single multiple logistic regression with all independent variables included, to assess the effect of each trait after the other variables have been factored out of the analysis. A multiple logistic regression with independent variables of species, sex, body size (SVL), time (day/night) and habitat (water/land) shows that whether or not a snake fled from the stimulus was affected by the time that it was tested (day/night, $\chi^2 = 32.94$, 1 df, $p = 0.0001$) and whether it was encountered in water or on land ($\chi^2 = 10.46$, 1 df, $p = 0.001$). As before, smaller snakes were more likely to flee ($\chi^2 = 9.80$, 1 df, $p = 0.002$), and males and females responded in similar ways ($\chi^2 = 0.002$, 1 df, $p = 0.97$). The strong interspecific difference evident in univariate analyses, however, disappeared almost entirely in the multivariate test ($\chi^2 = 0.18$, 1 df, $p = 0.66$). That is, *L. colubrina* fled from us less often not because it responded differently than *L. laticaudata*, but because we frequently encountered *colubrina* on land during the day (circumstances that stimulated crypsis) whereas we generally found *laticaudata* in water at night (circumstances that stimulated flight).

Discussion

Below, we focus on the two main issues raised in the Introduction: the degree to which interspecific differences in antipredator behavior are attributable to differences between the taxa in ecology (habitat, time of activity) rather than in antipredator responses *per se*; and the degree to which the observed antipredator responses accord with predictions based on the putative effectiveness of those tactics in different situations.

The two laticaudid species that we studied are broadly sympatric over a wide geographic range (Cogger 1975; Guinea 1994; Voris & Voris 1995) and often occur in close syntopy. We frequently found *L. colubrina* and *L. laticaudata* < 1 m apart, and sometimes in physical contact with each other. Nonetheless, we documented a strong difference in antipredator responses: 49% of *L. colubrina* fled from our approach, compared to 84% of *L. laticaudata*. Our multivariate analysis indicates, however, that the two species actually responded to us in very similar ways. The interspecific difference in the proportion of snakes fleeing was almost entirely due to divergence in the times and places that we encountered snakes (especially, the greater terrestriality and diurnality of *L. colubrina* than of *L. laticaudata*: Greer 1997), rather than intrinsic differences in antipredator responses between the two taxa. This result offers a cautionary tale. If we had not recorded information on habitats and times of encounter, we could have concluded that the two sympatric laticaudid species differ in antipredator tactics. The problem is likely to be exacerbated if the specific environmental cue that modifies antipredator responses is more subtle and thus, easily overlooked in a field study. The same issues are likely to arise for intraspecific divergence in antipredator behavior. For example, different age, sex and reproductive groups within a snake population are often active at different times and in different places (Bonnet & Naulleau 1996; Shetty & Shine 2002), and this ecological divergence might well generate considerable intraspecific diversity in antipredator responses.

Snakes demonstrate substantial flexibility in selecting antipredator responses (Greene 1988). Some of the characteristics that affect snake responses relate to the animal itself (e.g. its species, body size, coloration, sex, body temperature, whether or not it is gravid or has recently fed) whereas others involve the situation in which it encounters the predatory stimulus (e.g. proximity to cover, habitat type) (Duvall et al. 1985; Herzog & Bailey 1987; Brodie & Russell 1999; Fitch 1999; Shine et al. 2002). Additionally, these intrinsic and extrinsic factors can covary with each other in complex ways (Goode & Duvall 1989; Shine et al. 2000). Our study adds to this diversity, with data on a snake species that is geographically, phylogenetically and ecologically very different from most of the taxa upon which previous studies have been conducted.

The data on New Caledonian laticaudids support all four predictions outlined in the Introduction to this paper. The snakes that attempted to flee (rather than rely on crypsis) were those most able to move rapidly (i.e. juveniles rather than adults; and in water rather than on land) and in situations where a fleeing snake would be more difficult for a predator to capture (i.e. at night rather than during the day). In keeping with the lack of strong species or sex effects on locomotor speeds, neither of these factors affected antipredator tactics. These results support the optimality hypothesis that animals adopt behaviors that maximize their probability of surviving an encounter with a potential predator. The same hypothesis is consistent with many other patterns in snake antipredator behavior: for example, snakes are less likely to flee if their locomotor ability is compromised by factors such as low body temperature (Fitch 1965; Heckrotte 1967; Costanzo 1986; Passek & Gillingham 1997; Mori & Burghardt 2001), fatigue (Arnold & Bennett 1984), low body condition (Andren 1982), pregnancy (Goode & Duvall 1989), or a recent meal (Herzog & Bailey 1987), or if the feasibility of escape is influenced by the proximity of shelter or conspecifics (Duvall et al. 1985; Shine et al. 2002).

Although these effects suggest that snake antipredator behaviors are flexible responses to the relative effectiveness of alternative tactics in any given encounter, one major puzzle remains. This involves the snakes' general lack of response to harassment. Our results not only confirm previous anecdotal reports of the extreme reluctance of laticaudids to bite when harassed, despite their formidable venom (Heatwole & Guinea 1993), but also show that most snakes did not even attempt to flee from our approach. In these respects, they differ strongly from most other previously studied snake species (references above). Intuition suggests that laticaudid snakes should display active defence, but they almost never do so. Hence, although adaptationist interpretations accord well with intraspecific and interspecific patterns in response, the overall absence of more vigorous antipredator tactics remains surprising, and a challenge to any straightforward optimality-based explanation.

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