

Danger on the rise: diurnal tidal state mediates an exchange of food for safety by the bar-bellied sea snake *Hydrophis elegans*

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ABSTRACT: Prey vulnerability to predation can depend on abiotic conditions. Thus, prey individuals may adjust their investment in anti-predator defense according to changes in one or more abiotic factors. We explored this possibility in Shark Bay, Western Australia, where the bar-bellied sea snake *Hydrophis elegans* is under threat of predation by the tiger shark *Galeocerdo cuvier*, asking specifically whether the diurnal tidal state influenced snakes' selection of exposed foraging habitat (sand flat) and refuge habitat (seagrass). At high tide, when both habitats were easily accessible to sharks, *H. elegans* selected seagrass habitats, where its food is relatively scarce. At low tide, when sharks had limited access to both habitats, *H. elegans* used the 2 habitats equally but foraged exclusively over sand flats. We concluded that *H. elegans* is sensitive to the danger of tiger shark predation and trades food for the safety of a refuge when diurnal tidal conditions in its foraging habitat expose it to sharks. Our results suggest that predation risk should be considered in studies of sea snake habitat use and that important variation in predator–prey interactions may be missed if relevant abiotic conditions are ignored.

KEY WORDS: Abiotic factors · Foraging · *Galeocerdo cuvier* · *Hydrophis elegans* · Predation risk · Prey vulnerability · Tiger shark

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INTRODUCTION

Prey vulnerability to predation can show marked spatial and temporal variability (Lima 1998, Lima & Bednekoff 1999). This variation can correspond with changes in a host of abiotic conditions including diel state (e.g. Culp et al. 1991), dissolved oxygen concentration (e.g. Moore & Townsend 1998), habitat structure (e.g. Talman et al. 2004), moonlight (e.g. Griffen et al. 2005), precipitation (e.g. Ovadia & Schmitz 2004), salinity (e.g. Handeland et al. 1996), temperature (e.g. Weetman & Atkinson 2002) and water depth (e.g. Gawlik 2002). In many cases, therefore, we might expect the amount of anti-predator investment by prey individuals to correlate with fluctuations in one or more abiotic factors and overall levels of investment in

safety to be a function of the time that abiotic conditions render the environment dangerous (Lima & Bednekoff 1999, Hamilton & Heithaus 2001). Anti-predator behavior is often incommensurate with foraging, so variation in abiotic conditions that influence the need for anti-predator defense could influence exploitation rates of resources by prey species. Thus, studies of the interaction between abiotic conditions and anti-predator investment should lead to an improved understanding of community dynamics.

In marine systems the influence of abiotic conditions on interactions between sessile invertebrates and their predators has long been appreciated (Sousa 1984, Warner et al. 1993). The possibility that abiotic conditions mediate interactions between more mobile marine prey species and their predators has rarely

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been explored (e.g. Heithaus & Dill 2002, Hays 2003, Wirsing et al. 2007a), and no study to date has investigated this question using a sea snake as the model species. Accordingly, we asked whether diurnal tidal state influenced the use of exposed and refuge habitats in an Australian embayment (Shark Bay, Western Australia) by bar-bellied sea snakes *Hydrophis elegans* threatened with tiger shark *Galeocerdo cuvier* predation.

Hydrophis elegans is a large hydrophiid that occurs in coastal waters along northern Australia and southern New Guinea (Heatwole 1999). In Shark Bay, *H. elegans* has access to 2 nearshore habitats: shallow sand flats and seagrass meadows. Sand flat habitats are home to snake eels (Ophichthidae) (McCosker & Rosenblatt 1993), on which *H. elegans* appears to specialize (Kerford 2005), but are exposed and therefore offer little protection from sharks. In contrast, seagrass meadows offer little food but feature dense vegetation that promotes crypsis (M. R. Kerford pers. obs.) and likely provides a physical refuge from sharks (Orth et al. 1984). Both habitats are used by tiger sharks, which are a major consumer of sea snakes, including *H. elegans*, in Shark Bay (Heithaus 2001, Simpfendorfer et al. 2001) and elsewhere (Simpfendorfer 1992). During low-tide periods, however, tiger sharks are rarely sighted in either habitat (M. R. Heithaus unpubl. data, M. R. Kerford pers. obs.), likely because their mobility is restricted. Consequently, *H. elegans* may only incur a predation cost when using sand flats instead of seagrass meadows at high tide. This cost may be especially high for foraging snakes, which leave their

bodies vulnerable to attack while probing snake eel burrows (Kerford 2005).

We tested the hypothesis that *Hydrophis elegans* sacrifices food for safety when diurnal tidal conditions render its foraging habitat too risky. Under the assumptions that food (snake eel availability) is largely restricted to sand flats and that seagrass meadows act as a refuge for *H. elegans*, this hypothesis predicts that (1) relative use of seagrass meadow habitat should be greatest at high tide when the danger of predation in sand flat habitat is high and (2) foraging should occur primarily in sand flat habitats and during low tide when shark predators are virtually absent. Conversely, if *H. elegans* is insensitive to changes in tiger shark predation risk caused by tidal variation, then relative *H. elegans* abundance across the 2 habitats and forager abundance in sand flat habitat should be independent of tidal state.

MATERIALS AND METHODS

Study site. We conducted the present study between February and April 2004 in the Eastern Gulf of Shark Bay (ca. 25° 45' S, 113° 44' E; Fig. 1a), which lies at the southern extent of the distribution of *Hydrophis elegans* (Heatwole 1999). Shark Bay is remote, lightly populated and has been protected as a World Heritage Area since 1991. Consequently, it is considered to be relatively pristine. Its *H. elegans* and tiger shark populations are large and free from anthropogenic exploitation (Heithaus 2001, Kerford 2005, Wirsing et al. 2006).

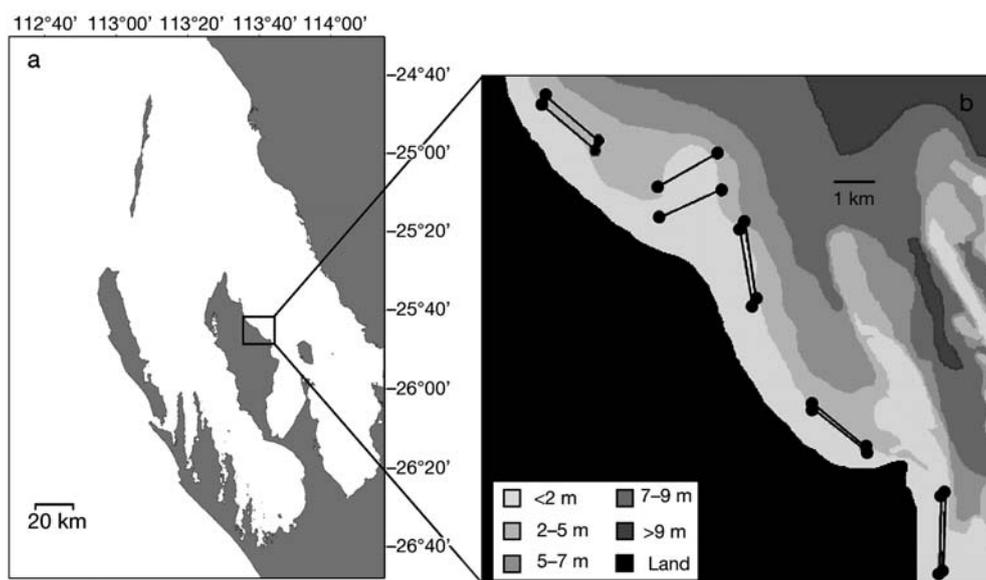


Fig. 1. The Eastern Gulf of Shark Bay, Western Australia (a) and paired transects (b) ($n = 5$ pairs) established in nearshore sand flat and seagrass habitats

Sea snake habitat use. We quantified the use of sand flat and seagrass meadow habitats by *Hydrophis elegans* using paired 2 km transects in 5 nearshore locations (Fig. 1b). At each location one transect was placed in sand flat habitat and the other in seagrass habitat. All seagrass transects bisected meadows comprising a mixture of 2 temperate seagrass species, *Amphibolis antarctica* and *Posidonia australis*, which predominate throughout much of the bay. These meadows were dense, continuous and extended to an average of 25 cm above the substrate (A. J. Wirsing unpubl. data), providing ample hiding possibilities and protective cover. At all locations seagrass transects were immediately offshore of sand flat transects, but depths were similar (generally ≤ 3.5 m). All transect pairs were separated by at least 100 m. Transects were surveyed by 2 observers driving a 4.5 m vessel at ca. 7 km h^{-1} ; no transect was visited on consecutive days, and the order of visitation on any given day was haphazard. Survey effort was allocated evenly to sand flat and seagrass meadow habitats (94 passes each). Moreover, effort was similar at high and low tide in both sand flats (47 passes each) and seagrass meadows (52 and 42 passes, respectively). Tidal state was recorded at the beginning of each transect. We considered low-tide transect passes to be those occurring when the predicted tidal height in Australian chart datum (height above lowest astronomical tide) fell below the mean value for the study area (1.40 m, Sargeant et al. 2005); high-tide passes occurred when the predicted tidal height exceeded this threshold. Actual measured depths at low tide averaged 1.32 m, while those at high tide averaged 3.13 m. During each transect pass we recorded all *H. elegans* sighted within 5 m of the vessel (i.e. within a 10 m sighting belt) and whether each individual was engaged in foraging or another behavior (resting or traveling). Foragers were defined as individuals actively probing the substrate with their heads or with their heads inserted into the substrate and their tails sticking up into the water column; swimmers were defined as individuals traveling through the water column without showing any interest in or making contact with the substrate, and resting individuals were those lying motionless on the ocean floor. Sea snakes were difficult to detect on cloudy and windy days. Thus, we only conducted transects on days when cloud coverage was $\leq 20\%$ and Beaufort wind conditions were ≤ 1 .

Tiger shark abundance. The abundance of tiger sharks in the study area fluctuates seasonally (Wirsing et al. 2006). We assayed *Hydrophis elegans* habitat use during the Austral warm season when local shark numbers typically are high, and this pattern persisted in 2004 (Wirsing et al. 2006). Therefore, the need for sea snakes to invest in anti-predator defense presumably was great during the course of the present study.

Importantly, other sympatric species that are subject to predation by tiger sharks invested heavily in anti-predator behavior during the months in which the present investigation took place (e.g. bottlenose dolphins *Tursiops aduncus*, Heithaus & Dill 2002; dugongs *Dugong dugon*, Wirsing et al. 2007a,b).

Statistical analysis. For all snakes and forager-only groups, we typically encountered no more than 1 individual per transect run. Consequently, our dependent variables (snake and forager sighting frequency) were best expressed as a binomial, leading us to model them using logistic regression. For the model of overall *Hydrophis elegans* abundance, we made habitat type (sand flat versus seagrass), tidal state (high versus low) and the interaction between these 2 factors available for inclusion as predictor variables. In addition, the transect was included as a blocking factor to account for spatial heterogeneity in the observations. For the model of forager abundance, data from transect passes over seagrass habitat were not analyzed, and only tidal state and transect served as predictor variables because foraging was not observed over seagrass in spite of 94 transect passes through this habitat type. Relationships were considered significant at $\alpha = 0.05$ for both models.

RESULTS

We sighted a total of 63 individual *Hydrophis elegans*, 14 of which were engaged in foraging. Overall, tidal state and the interaction between habitat and tidal state were significant predictors of *H. elegans* abundance (Table 1). Snakes were sighted significantly more frequently in seagrass habitat than in sand flat habitat at high tide, while sighting rates in the 2 habitats did not differ at low tide (Fig. 2). Foraging snakes only were encountered in sand habitats and the probability of sighting a foraging snake differed significantly according to tidal state (Table 2), with this behavior occurring primarily at low tide (12 of 14 cases, Fig. 3).

Table 1. Logistic regression analysis of the influence of habitat (sand flat versus seagrass), tidal state (high versus low), transect (spatial heterogeneity) and the interaction between habitat and tide on the probability of sighting bar-bellied sea snakes *Hydrophis elegans* along 2 km transects. Significant values are shown in bold.

Variable	β	Odds ratio	<i>t</i> -ratio	<i>p</i>
Habitat	-0.25	0.78	-0.56	0.578
Tide	-1.38	0.25	-2.61	0.009
Transect	0.23	1.26	1.84	0.066
Habitat \times Tide	1.87	6.51	2.71	0.007

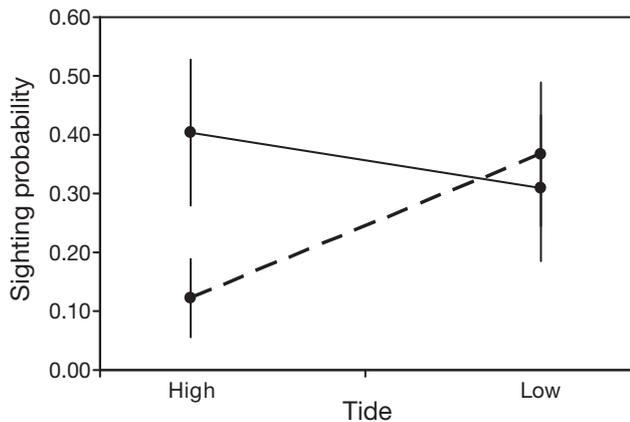


Fig. 2. *Hydrophis elegans*. Relative abundance, all snakes (estimates of sighting probability $\pm 95\%$ confidence intervals, transects pooled) in sand flat (dashed line) and seagrass (solid line) habitats at high and low tide

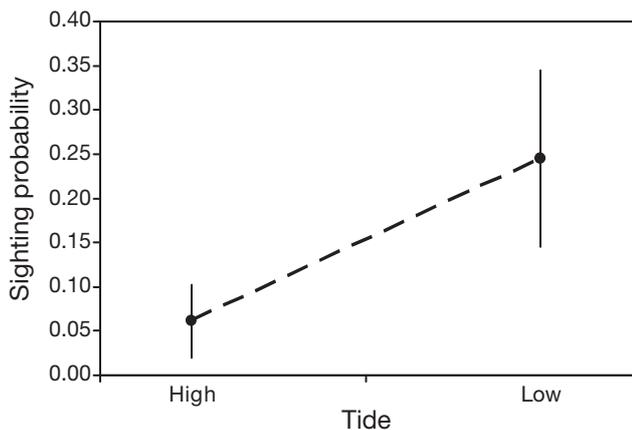


Fig. 3. *Hydrophis elegans*. Relative abundance, foraging snakes only (estimates of sighting probability $\pm 95\%$ confidence intervals, transects pooled) in sand flat habitat at high and low tide. No foraging snakes were observed during 94 transect passes through seagrass habitats

DISCUSSION

Interactions between abiotic conditions and anti-predator investment by marine prey species are poorly documented despite the likelihood that they are prevalent. In the present study we showed that the sea snake *Hydrophis elegans* invests in anti-predator defense only when diurnal abiotic conditions necessitate safety-conscious behavior: in accord with our predictions, *H. elegans* selected seagrass (refuge) habitats over exposed sand flat habitats during high tide when the presence of tiger sharks was elevated, foraged exclusively in sand flat habitats and foraged primarily at low tide when the danger of shark attack was mini-

Table 2. Logistic regression analysis of the influence of tidal state and transect on the probability of sighting foraging *Hydrophis elegans*. Includes only sightings over sand flats because foraging was not observed over inshore seagrass meadows

Variable	β	Odds ratio	<i>t</i> -ratio	<i>p</i>
Tide	-1.56	0.21	-2.27	0.023
Transect	0.24	1.27	1.08	0.280

mal. These results have important implications for our understanding of sea snake habitat use, the ecological role of large sharks in nearshore marine ecosystems, use of shallow coastal habitats in Shark Bay by tiger sharks and studies of anti-predator behavior that do not consider the possible role of abiotic factors in mediating predator-prey interactions.

Habitat use by sea snakes has been studied rarely (e.g. Burns & Heatwole 1998). Moreover, no study to date has explored the habitat choices of a sea snake species in the context of predation risk, though Shine et al. (2003) postulated that immature turtle-headed sea snakes *Emydocephalus annulatus* might use shallow, inshore waters (<1 m in depth) as a means to escape shark predation. Our results reveal that the threat of predation can affect sea snake patch use decisions, eliciting the abandonment of otherwise profitable foraging habitats during dangerous time periods. Such sacrifices by sea snakes are likely ubiquitous given that the ranges of many sea snake species overlap with those of sharks for which they are regular prey (e.g. *Galeocerdo cuvier* and *Carcharhinus melanopterus*, Lyle & Timms 1987). Consequently, we suggest that future studies of sea snake habitat use that ignore the potential influence of shark predators may yield erroneous results and that explicit consideration of shark predation danger by such studies should lead to an improved understanding of sea snake ecology.

Our results also reveal that some *Hydrophis elegans* individuals are willing to use exposed foraging habitat when sharks are present. While foraging primarily occurred at low tide, 2 individuals were sighted foraging over sand at high tide. Though an explanation for this risk-taking behavior will require further analysis, we suggest that it may be the result of depressed condition. That is, individual snakes in poor condition with few assets to protect may be willing to expose themselves to danger in order to exploit food resources during periods when individuals in better condition opt for safety (Clark 1994).

The tight fit between our predictions and the results of this analysis suggests strongly that tiger shark predation risk was responsible for the observed habitat

shifts by *Hydrophis elegans*, but other possible explanations do exist. For example, smaller sharks, changes in temperature or reduced snake eel (i.e. food) availability might have induced *H. elegans* to avoid sand flat habitats at high tide. Furthermore, our results could have been an artifact of differences in our ability to detect sea snakes in sand flat and seagrass habitats. We consider these possibilities to be unlikely because (1) the small shark species commonly observed in the present study area (the milk shark *Rhizoprionodon acutus* and nervous shark *Carcharhinus caudatus*) are not major predators of sea snakes (White et al. 2004), (2) water temperature differences between tidal states were not detected (Kerford 2005), (3) foraging over sand flats at high tide by *H. elegans* was observed both during transect passes and focal animal follows (Kerford 2005), rejecting the explanation that snake eels are only available at low tide, and (4) foraging and traveling *H. elegans* were easy to spot in both habitats under all conditions (Kerford 2005), and the likelihood that we missed sea snakes resting or hiding in seagrass habitats does not confound our results because the visibility of such individuals did not vary with tide (20 sightability trials per tidal state, 5 recumbent sea snake decoys deployed haphazardly along a seagrass transect per trial; $t_{38} = -0.16$, $p = 0.877$). Furthermore, if there was marked variation in sighting efficiency in seagrass habitats, more snakes should have been observed in this habitat at low tide; however, the opposite trend was found.

Our conclusions also rest on the assumptions that snake eels are indeed found predominantly in sand flat habitat and that seagrass serves as a protective refuge for sea snakes. We are confident in the first assumption because an intensive survey of both habitats revealed an abundance of burrows in sand flat habitat (mean \pm SE = 87.6 ± 15.1 burrows m^{-2}) and no evidence of eel burrowing activity (i.e. presence) in substrate covered by seagrass (ANOVA, $F_{3,84} = 5.29$, $p = 0.002$). The second assumption is corroborated by our finding that decoy sea snakes placed within seagrass habitat are highly cryptic and often difficult to retrieve (mean \pm SE = 1.1 ± 0.8 decoys retrieved out of 5 during sightability trials) relative to those over sand habitat (3.2 ± 0.9 decoys retrieved) ($t_{38} = 7.90$, $p < 0.001$) and the fact that our attempts to follow sea snakes in seagrass habitats were often frustrated by snakes moving entirely under the seagrass canopy.

The ecological role of large sharks is hotly debated, largely because few studies have documented interactions between sharks and their prey that might trigger changes in marine community structure (Heithaus 2008). A small but growing body of evidence, however, suggests that large sharks may exert strong top-down effects on marine communities. For example, Myers et

al. (2007) argue that the collapse of the bay scallop *Argopecten irradians* fishery off North Carolina, USA, was the result of a numerical increase in their elasmobranch predators due to a large decrease in shark abundance. Furthermore, in Shark Bay, Western Australia, tiger sharks influence the spatial pattern of herbivory by large grazers (the green sea turtle *Chelonia mydas* and dugong *Dugong dugon*) and may therefore indirectly affect seagrass meadow composition and structure (Heithaus et al. 2007, Wirsing et al. 2007a,b). The present study suggests that tiger sharks hinder *Hydrophis elegans* from exploiting snake eels in nearshore sand flat habitats at high tide and, as a result, provide snake eels with a temporal refuge from predation. By inference, then, any change in the use of inshore habitats by sharks could alter the temporal pattern of predation pressure imposed by *H. elegans* on snake eels in a manner that could induce community restructuring. Studies addressing this possibility should enhance our understanding of the top-down role of large sharks in Shark Bay and other inshore systems where sharks and sea snakes coincide.

The high frequency of occurrence of sea snakes in the stomach contents of tiger sharks in Shark Bay led Heithaus (2001) to suggest that seasonal variation in tiger shark abundance in the bay's Eastern Gulf might be linked in part to the availability of sea snakes. A comparison of sea snake and tiger shark numbers in offshore habitats within the current study area provided no support for this hypothesis (Wirsing et al. 2007c). The results of the present study, however, suggest that such a link could exist in Shark Bay's shallower, nearshore habitats. Indeed, tiger sharks and sea snakes may be engaged in a habitat use game in these areas, with sharks seeking to catch snakes willing to forage at tidal levels above the threshold of safety and snakes seeking to maximize their energetic intake rates without crossing this threshold. A more detailed analysis of individual movements across the tidal gradient for both species will be required to answer this question.

The outcomes of species interactions are often influenced by abiotic factors (Warner et al. 1993, Martin 2001). Consequently, studies of these interactions that fail to consider abiotic conditions may yield incomplete or spurious results. Had the present study not explicitly considered the rise and fall of the tide, for example, we would have completely missed the effect of tiger sharks on the habitat use and foraging behavior of *Hydrophis elegans*. We conclude, therefore, that an increased focus on interactions between abiotic factors and defensive investment by prey will improve our ability to detect and predict species responses to and the top-down effects of predators across marine systems and taxa.

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