

# Olive-headed sea snakes *Disteria major* shift seagrass microhabitats to avoid shark predation

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**ABSTRACT:** Predators elicit prey spatial shifts that may influence prey resources. The nature of these indirect effects is difficult to predict, however, in part because the means by which prey differentiate safe from dangerous space are poorly understood. Prey often avoid their predators, but they may instead favor predator-rich areas that facilitate escape, or discourage attack, when a predator is encountered. We investigated how olive-headed sea snakes *Disteria major* index their risk of tiger shark *Galeocerdo cuvier* predation over seagrass bank microhabitats (edges, interiors) in Shark Bay, Australia. *D. major* is equally likely to escape sharks in both microhabitats, so we expected to observe avoidance of predator-rich space. Supporting our prediction, snakes used microhabitats roughly in proportion to food supply when sharks were scarce and avoided edges, which are preferred by sharks, when sharks were abundant. Thus, *D. major* appears to measure danger across seagrass banks using variability in predator density and to seek low-encounter microhabitats when anti-predator investment is needed. Our results suggest that the influence of predators on sea snakes is underappreciated and, in the context of previous work, that sympatric prey species sharing predators may show opposite spatial shifts when threatened, potentially leading to different predator indirect effects.

**KEY WORDS:** Anti-predator behavior · Predation risk · Predator indirect effects · Prey escape tactics · Tiger shark

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## INTRODUCTION

When confronted with danger, prey individuals often choose safe locations where energy is less available (Lima & Dill 1990, Lima 1998, Brown 1999, Brown & Kotler 2004). These spatial shifts redistribute patterns of prey foraging and ultimately help to organize communities (Schmitz et al. 2004), so they have received much attention (see reviews by Werner & Peacor 2003, Preisser et al. 2005, Verdolin 2006, Wirsing et al. 2008). Yet, few studies have asked how prey actually identify space where the threat of predation is low (see Lima & Valone 1991, Heithaus & Dill 2006, Wirsing et al. 2007, for examples) despite a call for such inquiries some time ago (Lima & Dill 1990), impeding the formulation of a general framework for predicting prey behavioral responses, spatial changes in the exploitation of prey

resources, and community structure following the imposition of predation risk. Studies of this nature are of particular interest in marine systems, where our understanding of the consequences of predation risk for prey behavior and communities lags behind that in terrestrial systems. Here, we explored the discrimination of safe from dangerous seagrass microhabitats by olive-headed sea snakes *Disteria major* under threat of predation by tiger sharks *Galeocerdo cuvier* in Shark Bay, Australia.

Predation risk in any given location is the product of the probability of encountering a predator and the probability of being killed following an encounter (Hugie & Dill 1994). Thus, although prey are generally assumed to avoid encounters with predators (i.e. to select space where predator abundance is relatively low; Lima 1992, 1998), individuals seeking to differen-

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tiate safe and dangerous areas can in fact rely on information pertaining to one or both of these components of risk. In situations where the probability of capture is spatially uniform, we would expect safety-conscious prey individuals to select locations where predators are scarce and encounter rates are relatively low when there is need for anti-predator investment (i.e. when predators are present in the environment; Lima 1992).

In Shark Bay, *Disteria major* forages diurnally for small teleosts over shallow, offshore seagrass banks (1.5 to 4.5 m in depth) that are surrounded by largely unvegetated deeper waters (6 to 12 m; Kerford 2005). The fishes on which *D. major* subsists are evenly distributed over these seagrass banks (based on species counts in fish traps, see Heithaus & Dill 2006), but predation risk is not. Instead, habitat use patterns of tiger sharks, the only major local sea snake predator (Heithaus 2001), indicate that they are more likely to be encountered along the periphery of seagrass banks (edge microhabitats) than at their center (interior microhabitats; Heithaus et al. 2006). Following encounters with predators over seagrass banks, *D. major* escapes into the vegetation (A. Wirsing pers. obs.), which provides a structural refuge (Kerford 2005, Kerford et al. 2008). Because seagrass is equally available and accessible in both microhabitats (Wirsing et al. 2007), *D. major* should use spatial variation in predator encounter rates rather than the probability of escaping tiger sharks to identify safe microhabitats while over shallow banks. The overall need for anti-predator investment by prey at risk from tiger sharks is not temporally constant, however, because shark numbers vary periodically between a high during the warm season (February) and a low during the cold season (July; Wirsing et al. 2006). Consequently, under the assumptions that *D. major* is sensitive to the threat of predation and acquires energy from any location at a frequency-dependent rate because of intra-specific competition, we expected to observe a preference for interior seagrass microhabitats (i.e. low predator encounter rates) that varies in strength with fluctuations in shark abundance. Specifically, we predicted that competition would lead *D. major* to use edges and interiors in proportion to food supply when sharks were scarce and that the presence of sharks would induce disproportionate use of interior microhabitats (at the cost of lower per capita energy intake rates because of resource depletion or interference; van Baalen & Sabelis 1993).

## MATERIALS AND METHODS

**Study site.** We conducted this study between February and May of 2004 and 2006 in the Eastern Gulf of Shark Bay, Western Australia (~25°45' S, 113°44' E;

Fig. 1a,b), which lies along the southern periphery of the distribution of *Disteria major* (Heatwole 1999). Shark Bay is considered to be relatively pristine because it is isolated, sparsely populated, and protected as a World Heritage Area. The *D. major* and tiger shark populations it supports are large and not subject to exploitation by humans within the study area (Heithaus 2001, Kerford 2005, Wirsing et al. 2006), although movements of tiger sharks into pelagic waters of the Indian Ocean may subject them to fishing pressure (Heithaus et al. 2007a).

**Seagrass bank microhabitat use.** We assessed patterns of *Disteria major* abundance in edge and interior microhabitats using transect passes over 6 shallow seagrass banks (Fig. 1c). Transects were performed using a 4.5 m vessel driven at 6 to 9 km h<sup>-1</sup>. We recorded the exact position of all *D. major* sighted at the surface within 5 m of the transect line (i.e. within a 10 m sighting belt; mean ± SD belt area was 6.3 ± 0.6 ha) before being passed by the boat. Within each sighting belt, we defined edge microhabitats as areas with water depths between 2.5 and 4.5 m or <2.5 m but within 75 m of deep water (>4.5 m), and interior microhabitats as areas featuring water depths <2.5 m and >75 m from deep water (Heithaus et al. 2006, Wirsing et al. 2007); relative microhabitat areas in each belt were quantified using a georeferenced bathymetric map and GIS software (MapInfo Professional version 4.5). We ensured sampling consistency by distributing our effort (n = 129 transect passes) evenly across the 6 shallow banks (mean ± SD = 21.5 ± 4.3 passes bank<sup>-1</sup>), sampling days (n = 36; mean = 3.5 ± 1.6 transect passes d<sup>-1</sup>), and sampling months (mean = 20.0 ± 3.6 transect passes mo<sup>-1</sup>). The total area of each microhabitat sampled per day also was roughly equivalent (edge mean = 10.3 ± 5.0 ha; interior mean = 11.9 ± 6.4 ha). We did not visit particular transects more than once per day, chose the order and direction in which transects were driven haphazardly to minimize any effects of tidal and diel variation, and did not conduct transects when Beaufort wind conditions exceeded 1 to eliminate sighting bias caused by limited visibility in poor weather.

Our study area is home to 2 additional sea snake species: the bar-bellied sea snake *Hydrophis elegans* and the Shark Bay sea snake *Aipysurus pooleorum* (Kerford 2005). Though *Disteria major* and *H. elegans* feature a similar striping pattern, *H. elegans* favors shallow, inshore sand flats and has a much smaller head than *D. major*; *A. pooleorum* overlaps spatially with *D. major* but is rarely seen (n = 8 sightings over the course of the study) and is easily distinguished by its dark coloration (Kerford 2005). Importantly, all sea snake sightings where the species could not be determined were censored from the analysis.

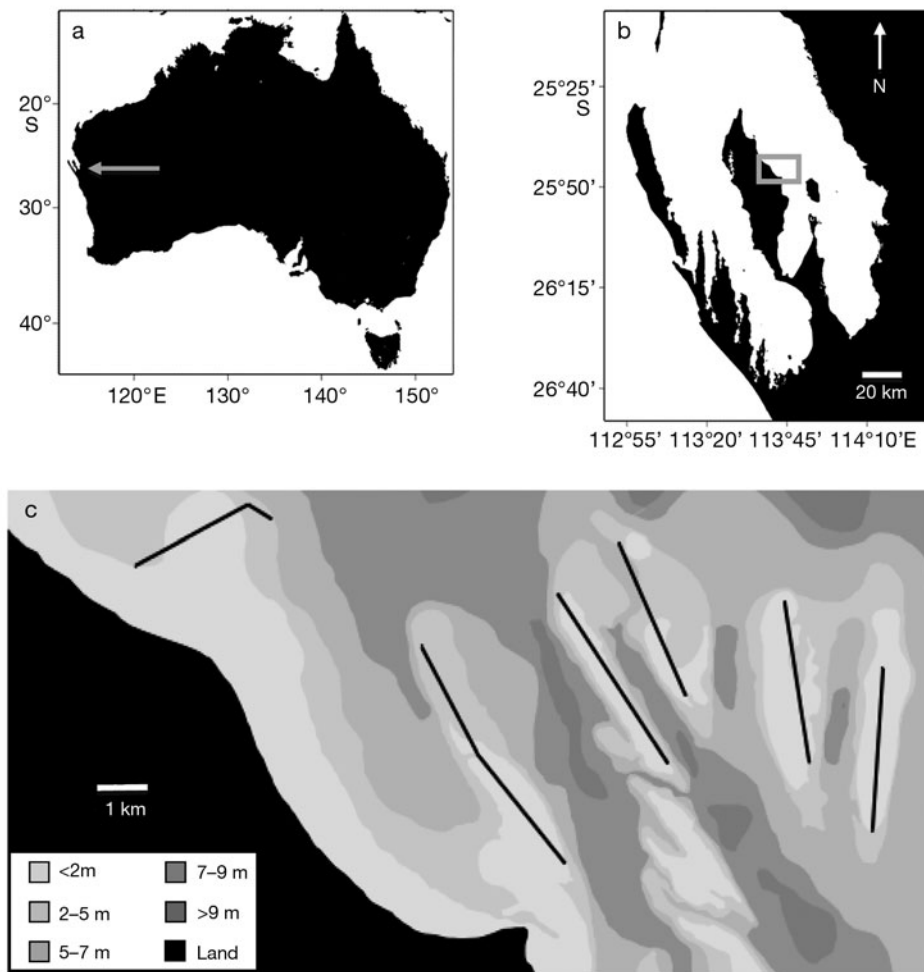


Fig. 1. Study site in Shark Bay, Western Australia (a; gray arrow). In our 160 km<sup>2</sup> study site in the Eastern Gulf (b; gray box), microhabitat use by the olive-headed sea snake *Disteria major* was assessed using belt transects (10 m wide, 3 to 4 km in length) over 6 shallow seagrass banks (c; shades of gray reflect variation in offshore water depth [m]). Land is shown in black

**Tiger shark abundance.** In both years of the study, *Disteria major* habitat use data were collected concurrently with an intensive tiger shark sampling effort using single-hook drumlines baited with Australian salmon *Arripis truttaceus* (see Wirsing et al. 2006 for methodological details). Catch rates on these drumlines reveal that, each year, tiger shark numbers decline steadily from peak levels (ca. 0.12 sharks caught per hour of hook soak time) in February to relatively low levels (ca. 0.03 sharks h<sup>-1</sup>) in May (Wirsing et al. 2006). Thus, we were able to conduct a ‘natural experiment’ (sensu Biro et al. 2005) during which the environment for *D. major* varied predictably from dangerous to relatively safe.

**Statistical analysis.** We calculated *Disteria major* microhabitat densities in transect sighting belts by dividing the number of snakes sighted in each micro-

habitat by the area of each microhabitat searched. Prior to analysis, we averaged densities for edge and interior microhabitats within all sighting belts visited on a given day; estimated densities for 3 d were ultimately excluded from the analysis because they were determined to be outliers (high leverage  $h_{ij}$  Kleinbaum et al. 1998). Since prey of *D. major* use both microhabitats equally (Heithaus & Dill 2006), we assumed that proportional use of edge and interior microhabitats after accounting for their relative areas signified input matching (i.e. a distribution driven by food availability), while underutilization of edges was assumed to signify an effect of predation risk on microhabitat choice (van Baalen & Sabelis 1993, Heithaus & Dill 2002). We built 2 competing models of *D. major* density. The first incorporated tiger shark abundance (sharks caught per hour fished) and the interaction

between microhabitat and shark abundance (to test for a shark-induced microhabitat switch) as independent variables. In our study area, tiger shark abundance and ocean temperature covary positively ( $r = 0.86$ ; Heithaus 2001), so we needed to ensure that any observed statistical link between shark abundance and *D. major* microhabitat use was legitimate rather than an artifact of underlying correlation between the density of these sea snakes and temperature. Thus, daily estimates of tiger shark abundance were replaced with daily temperature measures in the second model (note that variables for ocean temperature and shark abundance could not be evaluated in the same model because of their multicollinearity; Zar 1999). Both models also included variables for year (2004, 2006) and seagrass bank microhabitat (edge, interior). We fit the models using maximum-likelihood with a Poisson error distribution and a log link function because the dependent variable was expressed as a rate (i.e. counts divided by search area; Selvin 1995). We then ranked the models using Akaike's Information Criterion, corrected for small sample size ( $AIC_c$ ), and considered differences in  $AIC_c > 2$  to indicate substantial support for one model over the other (Burnham & Anderson 1998). In performing this non-nested model comparison, we assumed that superiority of the shark abundance-based model would indicate a real effect of predation risk on *D. major* microhabitat use, while superiority of the temperature-based model would imply that any apparent link between shark abundance and snake distribution was in fact spurious. Finally, in each model, we considered coefficients with 95% confidence intervals not overlapping zero to indicate a significant effect.

## RESULTS

We sighted 42 *Disteria major*, of which 26 were observed in 2004 and 16 were encountered in 2006. *D. major* sighting rates did not vary significantly across years, between bank microhabitats, and as tiger shark abundance changed (Table 1). The final model of *D. major* sighting frequency did, however, feature a significant interaction between microhabitat and shark abundance (Table 1); use of interior microhabitat exceeded that of edge microhabitat when shark abundance was high, but this disparity largely disappeared as shark abundance declined (Fig. 2).

The model of *Disteria major* sighting frequency in which measures of water temperature replaced those of predator abundance performed poorly relative to its counterpart (difference in  $AIC_c = 2.99$ , Table 1). Indeed, all of the relationships between the variables in this model and *D. major* sighting rate were non-significant.

Table 1. Competing generalized linear models of olive-headed sea snake sighting rate (snakes  $\text{km}^{-2}$  surveyed) based on (a) tiger shark catch rate (sharks  $\text{h}^{-1}$  fished, 'Shark') and the interaction between microhabitat and shark catch rate or (b) sea surface temperature ( $^{\circ}\text{C}$ , recorded daily at a constant location within the study site, 'Temp') and the interaction between microhabitat and sea surface temperature. Both models also accounted for the effects of year (2004, 2006) and seagrass bed microhabitat (edge, interior). A Poisson error distribution served as the basis for statistical inference, and coefficients with 95% confidence intervals not overlapping zero were deemed to indicate a significant effect. The shark-based model (a) is better supported (i.e.  $AIC_c$  score 2.99 below that of its counterpart; Burnham & Anderson 1998)

| Term                        | $\beta$ | 95% Confidence interval | Effect |
|-----------------------------|---------|-------------------------|--------|
| <b>(a)</b>                  |         |                         |        |
| Constant                    | -178.66 | -878.75, 521.43         |        |
| Year                        | 0.09    | -0.26, 0.44             | No     |
| Microhabitat                | -1.49   | -3.52, 0.55             | No     |
| Shark                       | -59.10  | -130.03, 11.84          | No     |
| Microhabitat $\times$ Shark | 102.94  | 21.73, 184.84           | Yes    |
| <b>(b)</b>                  |         |                         |        |
| Constant                    | -127.10 | -931.93, 677.73         |        |
| Year                        | 0.07    | -0.34, 0.47             | No     |
| Microhabitat                | -8.79   | -18.79, 1.20            | No     |
| Temp                        | -0.31   | -0.71, 0.09             | No     |
| Microhabitat $\times$ Temp  | 0.41    | -0.01, 0.84             | No     |

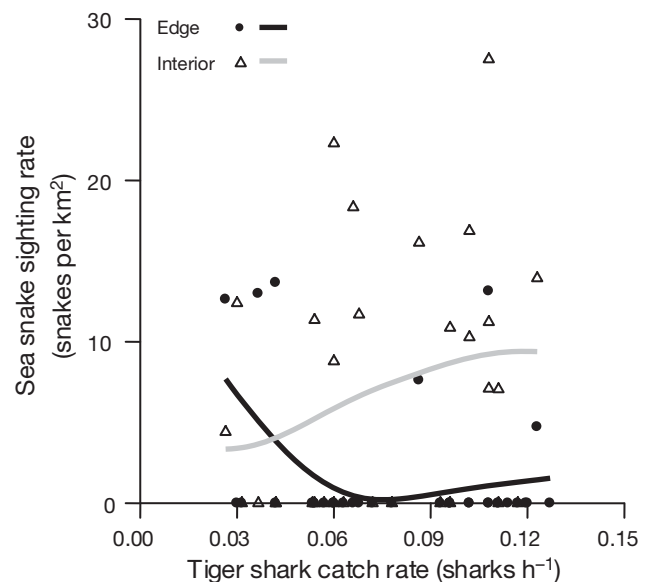


Fig. 2. *Disteria major* and *Galeocerdo cuvier*. Daily values for the relative use of edge and interior seagrass microhabitats by olive-headed sea snakes (snakes sighted per  $\text{km}^2$  surveyed) as a function of tiger shark abundance (sharks caught per hour fished). Trend lines were generated using distance-weighted least squares smoothing (DWLS, tension 1.0, SYSTAT 10.2)

## DISCUSSION

The results of this study suggest that *Disteria major* is sensitive to predation risk and discriminates between seagrass bank microhabitats based on the probability of encountering tiger sharks. *D. major* used edge and interior microhabitats evenly (i.e. roughly in proportion to food supply) when shark abundance was low but appeared to avoid edge microhabitats, which are preferred by tiger sharks (Heithaus et al. 2006), when shark numbers were elevated. This pattern of microhabitat use was not explained by changes in water temperature and is consistent with the theoretical expectation that, in the absence of predators, preference for safe space should diminish because of the availability of higher energy intake rates in riskier areas (van Baalen & Sabelis 1993). Thus, we can surmise that it is at least in part an anti-predator response. Our findings provide insights regarding the influence of predators on sea snakes and accurate prediction of predator indirect effects in communities.

Although sea snakes are commonly found in the stomach contents of tiger sharks in many locations (e.g. Simpfendorfer 1992, Heithaus 2001, Simpfendorfer et al. 2001), the possibility that predators influence their behavior has received little attention. However, Kerford et al. (2008) found that bar-bellied sea snakes *Hydrophis elegans* restrict their use of dangerous but resource-rich inshore foraging habitats to times when tidal conditions render them inaccessible to shark predators. Combined with their results, our finding that *Disteria major* avoid seagrass microhabitats that are patrolled heavily by tiger sharks suggests that predation risk-sensitive behavior may be widespread among sea snakes, at least in systems where large shark predators are still abundant (e.g. in the tropical waters off northern Australia). Consequently, we advocate additional scrutiny of sea snake-predator interactions, which will likely help to explain observed patterns of distribution and, insofar as anti-predator behavior can restrict reproduction (e.g. Creel et al. 2007), abundance. Furthermore, we suggest that in areas where shark numbers have been reduced, observed patterns of sea snake abundance, distribution, and foraging behavior may in some cases be an artificial reflection of diminished risk from predators.

Predators can indirectly influence community structure by altering prey behavior (Schmitz et al. 2004, Preisser et al. 2005, Creel & Christianson 2008, Heithaus et al. 2008), but the strength and nature of these indirect effects can be difficult to predict (Bolker et al. 2003, Werner & Peacor 2006). This difficulty owes in part to the context-specificity of behavioral interactions between predators and prey. For example, Schmitz (2008) found that the indirect effects spider

predators exerted on plant species diversity by altering grasshopper behavior in grassland mesocosms depended on predator hunting mode (and see also Preisser et al. 2007). Our ongoing work in Shark Bay and the results presented here suggest that the indirect effects of a predator employing a single hunting mode (in this case roving) could vary depending on the way its prey species can modify their risk of death across space. When present, tiger sharks hunt the perimeters of seagrass meadows, but their prey species do not uniformly avoid edge seagrass microhabitats during these time periods. Rather, bottlenose dolphins *Tursiops aduncus* (Heithaus & Dill 2006), dugongs *Dugong dugon* (Wirsing et al. 2007), and healthy green sea turtles *Chelonia mydas* (Heithaus et al. 2007b) increase their use of edge microhabitats (i.e. view them as safer than interior microhabitats) because they facilitate subsurface escape (Heithaus et al. 2006). Like pied cormorants *Phalacrocorax varius* (Heithaus et al. 2009), on the other hand, *Disteria major* cannot easily modify its chances of escape by changing location over seagrass meadows and therefore chooses interior microhabitats (avoidance) when there is need for anti-predator investment. Collectively, these results imply that tiger sharks could exert indirect effects on prey resources at different locations over seagrass meadows (i.e. edge versus interior microhabitats) that depend on the prey species being considered. For example, in edge microhabitats, tiger sharks could have a positive indirect effect on resources exploited by *D. major* and cormorants but a negative effect on those utilized by dolphins. Thus, a reliable framework for predicting predator indirect effects must consider not only responses to different predator hunting modes but also variability in the responses of sympatric prey species to each hunting tactic (see also Heithaus et al. 2009).

We acknowledge that, while changes in predation risk appear to drive a shift between seagrass microhabitats by *Disteria major*, other factors may have contributed to spatiotemporal variation in their abundance. In particular, higher predation rates on *D. major* by tiger sharks along the perimeter of seagrass meadows likely augment the disparity in sea snake density in edge and interior microhabitats when sharks are abundant. Consumption alone, however, is unlikely to be responsible for this disparity because *D. major* is a long-lived species (adults can live past 15 yr; Kerford 2005), suggesting a low mortality rate, and the decline in sightings along the edge was accompanied by an increase in sightings in interior microhabitats, implying a spatial shift. Differences in diving behavior also may have contributed to the drop in sightings along edges as shark numbers increased. Specifically, individual snakes in edge microhabitats may have reduced their relative time spent at the surface or their rate of



surfacing when sharks were numerous to minimize mortality risk (Heithaus & Frid 2003), exaggerating our estimation of the difference in use of the 2 microhabitats. We doubt that diving behavior was solely responsible for the apparent spatial difference in density during high-risk intervals, however, because a change in diving in edge microhabitats as shark abundance rose would not be expected to produce the observed increase in snake sightings in interiors. Finally, additional factors such as social interactions and reproduction will also have to be considered prior to the development of a complete understanding of the pattern of *D. major* microhabitat use that we observed.

In summary, our results underscore the need for additional work on sea snake–predator interactions and, when placed in the context of our continuing work in Shark Bay, help to explain why predator indirect effects in communities are often so complex; namely, because prey sharing the same predator and area can respond to variability in risk across space differently. We encourage further efforts to document inter-specific variation in risk perception by prey with shared predators, and venture that studies conducted in systems where escape and encounter probabilities are spatially asynchronous (i.e. where prey must choose between areas offering different types of safety; see Wirsing et al. 2007) and/or manipulate these 2 components of danger are likely to be particularly illuminating.

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