



Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators

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When threatened with predation, foraging prey can cease feeding and seek refuge or shift to feeding sites (microhabitats) offering increased safety. Predator-induced microhabitat shifts by large herbivores are of interest to ecologists because spatial patterns of foraging by these animals shape plant communities. The influence of predation risk on microhabitat use by large herbivores in marine systems remains poorly understood. We explored the relationship between microhabitat use by dugongs, *Dugong dugon*, and tiger shark, *Galeocerdo cuvier*, predation risk in an Australian embayment over 3 years. Use by foraging dugongs of two seagrass microhabitats, edge (lower-quality seagrass, swift escape from sharks) and interior (higher-quality seagrass, fewer escape options), was monitored in seven survey zones. We indexed predation danger using catch rates of tiger sharks that were greater than 3.0 m in total length. The degree of dissimilarity between forager densities in edge and interior microhabitats was a function of tiger shark abundance: foragers underused edge (safe) microhabitat when sharks were scarce, overused it when sharks were common, and responded to daily changes in shark abundance in a threat-sensitive fashion, showing the greatest preference for edges when shark abundance was highest. We conclude that dugongs manage their probability of death by allocating more time to safe but lower-quality feeding microhabitats when the likelihood of encountering sharks is elevated. Dugong grazing can influence seagrass biomass and patch composition, so tiger sharks probably affect the microhabitat structure of seagrass meadows, and ultimately their benthic communities, indirectly by altering the way that dugongs use feeding patches.

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Prey animals often make the costly decision to abandon foraging habitats in search of refuge when confronted with predation danger (Sih 1987; Lima & Dill 1990; Lima 1998). Such costs can be reduced if microhabitat variation within patches enables prey to adjust their mortality risk while continuing to acquire resources (Lima & Dill 1990). For example, prey under threat of predation may continue to forage without paying heavy fitness penalties by selecting feeding microhabitats facilitating crypsis, surveillance, escape, or access to refuges (Lima & Dill 1990; Lima 1998). Ecologists are keenly interested in predator-

induced microhabitat shifts by large herbivores (Schmitz et al. 2004), because spatial patterns of foraging by these animals may influence plant communities (Crawley 1983; Danell & Bergström 2002). In marine systems, the influence of predation danger (i.e. nonconsumptive predator effects) on large herbivore microhabitat use is poorly understood (Dill et al. 2003).

The nonconsumptive effects of predators on prey microhabitat use can be assessed using ideal free distribution (IFD) theory (Fretwell & Lucas 1970). IFD theory predicts that, if predation risk does not affect microhabitat use by foraging prey, then consumers should allocate their time to microhabitats in proportion to food supply such that each experiences the same payoff (i.e. intake rate). Under this scenario, food supply determines relative use of particular microhabitats by the consumer population, and forager densities in all microhabitats should be

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equivalent after correcting for food availability (e.g. by dividing consumer densities by the amount of food that each microhabitat offers). Alternatively, if predation risk influences microhabitat selection, then individual foragers should allocate more time to safe microhabitats than predicted by food availability when there is need for antipredator investment (e.g. when predators are abundant), causing corrected forager densities in these microhabitats to exceed those in more dangerous ones (van Baalen & Sabelis 1993). By extension, spatial differences between forager densities that emerge when the need for antipredator investment is high and that persist after accounting for variance in food supply can not only serve to identify the microhabitat perceived to be safe but also serve as a proxy for the amount of food that foragers sacrifice by avoiding dangerous microhabitat (i.e. the degree to which fear varies across space) (Brown & Kotler 2004). Importantly, this theoretical framework assumes that individual predators do not shift freely between microhabitats in response to their prey (sensu Hugie & Dill 1994). This assumption is valid when predators have diverse diets, which effectively fix predator distributions relative to specific prey species (Heithaus 2001b).

Following this framework, we explored patterns of microhabitat selection by dugongs, *Dugong dugon*, foraging on seagrass under risk of tiger shark, *Galeocerdo cuvier*, predation in Shark Bay, Western Australia. In Shark Bay, seagrass grows in meadows found primarily in shallow habitat (<4.5 m deep; Walker et al. 1988) that can be divided into edge and interior microhabitats (Heithaus et al. 2006). Edge microhabitats fall along the periphery of seagrass patches, and therefore offer increased water volume (depths generally 2.5–4.5 m) and swift access to deep habitat (>6.5 m). Consequently, dugongs encountering predators in these microhabitats are presumably better able to manoeuvre and escape to deeper water, where tiger sharks are scarce and more easily evaded (e.g. Heithaus et al. 2002), than are dugongs in interior microhabitats (Heithaus et al. 2006). However, tiger sharks hunt preferentially in edge microhabitats relative to interior ones (Heithaus et al. 2006).

Furthermore, nutrient composition of the seagrass species forming the bulk of the dugong's diet in our study area (*Amphibolus antarctica*) varies across the two microhabitats. Specifically, concentrations of organic carbon, a nutrient of alleged importance to dugongs (de Longh et al. 1995; Preen 1995), are elevated in interior microhabitats (Heithaus et al., in press). Thus, although dugongs are presumably less vulnerable to capture in edge microhabitats, they are less likely to encounter sharks and may be better able to acquire high-quality food while using interiors.

In any microhabitat, a forager's overall risk of death can be divided into its likelihood of encountering a predator and its probability of escape once attacked (Hugie & Dill 1994; Brown 1999; Luttbeg & Sih 2004). However, the relative extent to which foragers use these two components of risk to index safety when they are spatially uncorrelated has rarely been addressed (e.g. Heithaus & Dill 2006). Accordingly, we tested the hypothesis that dugongs manage their risk of mortality by using foraging microhabitats perceived to be safe, relative to those perceived to be

dangerous, in proportion to overall predator abundance (i.e. the need for antipredator investment) (predation risk sensitivity hypothesis). If dugongs index safety primarily in terms of their probability of escape, then this hypothesis predicts that, after correction for relative food supply, the degree of dissimilarity between foraging dugong densities in safe (edge) and hazardous (interior) microhabitats will be linked to predator (tiger shark) abundance, with foragers showing the strongest preference for edge microhabitats during periods of peak shark abundance (when the need for antipredator investment is greatest) and no microhabitat preference when sharks are scarce. If dugongs perceive safety chiefly in terms of predator density, then this hypothesis predicts that foragers should prefer interior microhabitats when sharks are abundant and lack a microhabitat preference when sharks are scarce. Alternatively, predation danger may not influence foraging dugong microhabitat use, in which case foragers should consistently (1) distribute themselves across the two microhabitat types in proportion to food supply (i.e. input match; van Baalen & Sabelis 1993) (food quantity hypothesis), or (2) overuse interior microhabitats if the seagrass available along meadow edges is nutritionally inferior (food quality hypothesis).

MATERIALS AND METHODS

Study Site

We undertook this study in the Eastern Gulf of Shark Bay (~25°45'S, 113°44'E; Fig. 1). Shark Bay is home to a large population of dugongs (10 000–14 000 individuals; Marsh et al. 1994; Preen et al. 1997; Gales et al. 2004), but their use of our study area fluctuates seasonally (Wirsing et al., in press a). In 1991, Shark Bay was listed as a World Heritage Area, and anthropogenic activity in the region has always been minimal. Thus, we were able to evaluate the microhabitat use of dugongs belonging to a healthy population under relatively pristine conditions.

Sampling Zones

We defined edge microhabitats as portions of shallow banks with water depths between 2.5 and 4.5 m and less than 2.5 m but within 75 m of deep water (>4.5 m), and interior microhabitats as areas featuring water depths less than 2.5 m and more than 75 m from deep water. We selected these microhabitat designations because (1) they are each well represented and (2) we assumed that dugongs occupying them are differentially able to manoeuvre and escape to deep (refuge) patches while under attack from tiger sharks (Heithaus et al. 2002, 2006). Our assumption that dugongs are less able to manoeuvre in interior microhabitats is supported by their behaviour: dugongs pursued by boats in shallow water (<2.5 m deep) have more difficulty changing direction than do those in water between 2.5 and 4.5 m deep (A. Wirsing, personal observation). We are confident that dugongs perceive deep patches as refuges because (1) foragers use them heavily when sharks are abundant even though they offer little food (Wirsing et al., in press a) and

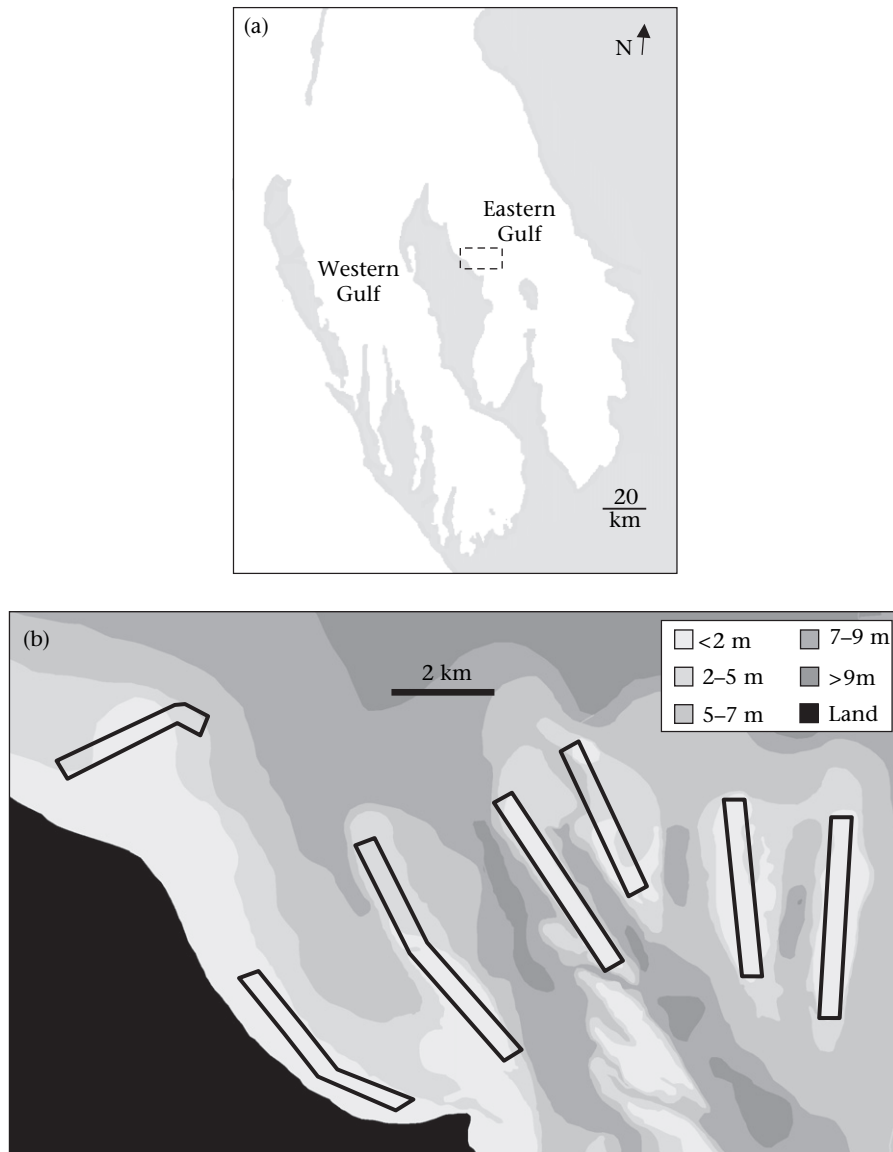


Figure 1. (a) Map of study site in the eastern Gulf of Shark Bay, Western Australia. (b) Survey zones (i.e. 400-m sighting belts; $N = 7$) were stratified evenly across shallow seagrass habitats throughout the study area (160 km²).

(2) dugongs that are approached rapidly by boats and by potential predators consistently flee from shallow to deep water (A. Wirsing, personal observation). We quantified edge and interior microhabitats in seven survey zones (mean \pm SD sampling area = 141.27 \pm 26.17 ha), each allocated to a discrete seagrass patch in shallow habitat (≤ 4.5 m in depth; Fig. 1b), using a georeferenced bathymetric map and GIS software (MapInfo Professional version 4.5, MapInfo Corporation, Toronto, Ontario, Canada). Edge microhabitat made up between 16.7% and 83.7% of the total sampling area for each survey zone (mean \pm SD = 52.4 \pm 24.8%).

Food Availability

We quantified food availability (biomass) within each survey zone using sampling stations positioned at 200-m intervals along a central transect line, as well as along

parallel lines 100 and 200 m to either side (75–120 stations per zone). At each station, a diver estimated seagrass species coverage and composition within a 1-m² quadrat. Seagrass height (cm) was also measured within the quadrat; we selected the point of measurement randomly to minimize bias stemming from height variability. Sampling occurred during the winter of 2003 (August–September), when herbivore densities were low, to minimize the confounding influence of herbivory and shark hazard to divers.

We expressed food biomass as above-ground seagrass volume (area covered \times height; m³); measures from sampling points within edge and interior microhabitats were pooled to generate overall values for each survey zone. Microhabitat volume measures for all zones consisted of two seagrass species: *A. antarctica* (mean = 82.71% of total volume) and *Posidonia australis* (mean = 17.29% of total volume). The value of *P. australis* as a dietary item for dugongs

is unknown, so we may have incurred bias by including it in our estimates of food supply. The removal of this species from consideration, however, did not affect the results reported later. Although we may also have incurred bias by failing to measure rhizomal (i.e. subsurface) biomass (de longh et al. 1995), such bias was probably modest since rhizomes of *A. antarctica* are unavailable to dugongs as food (Anderson 1986). Finally, our biomass samples did not include tropical seagrass species (e.g. *Halodule uninervis*), which are favoured by dugongs elsewhere (Preen 1995), because sampling occurred during the cold season when biomass of these species is low (Anderson 1986). Nevertheless, we consider our measure of food availability within the two microhabitats to be robust because tropical species are always scarce in our study area (Walker et al. 1988).

Dugong Density and Microhabitat Use

We assessed patterns of dugong abundance in each microhabitat using transect passes through the seven survey zones from 2002 to 2004. To ensure sampling consistency, we distributed our transect effort evenly across days ($N = 114$; mean \pm SD = 3.79 ± 1.64 passes/day), and months (22.85 ± 9.36 passes/month); overall, the area of each microhabitat surveyed per day was roughly equivalent (edge mean \pm SD = 249.23 ± 104.91 ha; interior mean \pm SD = 239.65 ± 105.07 ha). We did not visit particular survey zones more than once per day, and the order and direction in which transects were driven each day were haphazard to reduce the effects of tidal and diel variation. We did not conduct transects when Beaufort wind conditions exceeded 2 to minimize sighting bias caused by poor visibility in bad weather.

We performed transect passes using a small (4.5-m) vessel driven at 6–9 km/h. When dugongs were sighted at the surface within 200 m of the transect line (i.e. within a 400-m sighting belt) before being passed by the boat, we determined their exact position, using a GPS, and their behavioural state (foraging, resting, travelling), via direct observation and diagnostic surface behaviour (Anderson 1986; Chilvers et al. 2004; Wirsing et al., in press a). We distinguished dugongs using scarring patterns (Anderson 1995) and only counted individuals once per day; intra-annual resampling was rare.

Predator Abundance

Catch rates index tiger shark abundance in Shark Bay (Heithaus 2001b; Wirsing et al. 2006). We caught sharks using drumlines equipped with a single hook, baited primarily with Australian salmon, *Arripis truttaceus*, and deployed at dawn in six fishing zones within the study area; we measured (total length, TL), tagged and released all sharks caught throughout the day (for methodological detail, see Heithaus 2001b). Because of ontogenetic shifts in tiger shark diets (e.g. Lowe et al. 1996), tiger sharks less than 3.0 m long are unlikely to pose a threat to dugongs. Consequently, we only used sharks that were longer than 3.0 m to calculate daily catch rates.

Our fishing effort was intensive and temporally consistent (Wirsing et al. 2006). However, our fishing frequency (~ 6 fishing days/month) precluded continuous (daily) evaluation of the relationship between dugong habitat use and predator prevalence. Thus, given the strong seasonal pattern in shark abundance in the study area (Heithaus 2001b), we used a sinusoidal function with a period of 1 year to predict the annual trend in daily catch rates (sharks/h). We combined catch data used in the model for the years 2002–2004 because interannual variation was not detected after accounting for seasonal effects ($F_{2,117} = 0.97$, $P = 0.38$). We fit the model using maximum likelihood under the assumption of a Poisson error distribution because our data consisted of integer values for the number of sharks caught per day. To assess the validity of the model's predictions, we ran a companion analysis incorporating raw shark catch rates and dugong densities pooled across months. The results of this analysis were equivalent to those presented below.

Statistical Analysis

We calculated foraging dugong densities for individual survey zones by dividing the number of animals sighted by the area searched (ha). After blocking for spatial (survey zone) effects, seagrass biomass did not differ between microhabitats ($F_{1,599} = 0.20$, $P = 0.65$). Thus, for any survey zone, we assumed that proportional use of the two microhabitats after adjusting for their relative areas signified input matching (i.e. distributions driven solely by food supply), and that the degree to which forager densities in one microhabitat exceeded those in the other measured the effect of predation danger on microhabitat choice (van Baalen & Sabelis 1993; Heithaus & Dill 2002). We averaged densities for edge and interior microhabitats within all survey zones visited on a given day before analysis. We sighted six mother–calf pairs engaged in foraging while conducting transects. We treated these pairs as one individual because the behaviour of dugong calves is constrained by that of their mother.

We used information-theoretic methodology (Burnham & Anderson 1998) to explore the relation between predator abundance and foraging dugong microhabitat use. This approach ranks models of the relation between dependent and explanatory variables according to fit, while accounting for differences in complexity, and therefore facilitates rigorous evaluation of competing hypotheses (Burnham & Anderson 1998; Anderson et al. 2000; Johnson & Omland 2004). We evaluated four primary models of forager density: (1) a model based on shark abundance (S), to test whether fluctuation in predator numbers corresponded with changes in forager density but not with a microhabitat shift or a microhabitat preference (i.e. to challenge the food quantity hypothesis); (2) a model incorporating shark abundance and microhabitat category (edge versus interior; M), to test whether foragers consistently overused one microhabitat after accounting for changes in dugong and predator abundance (i.e. to challenge the food quality hypothesis); (3) a model including shark abundance and its interaction with microhabitat

category ($M*S$), to test whether fluctuation in predator numbers was accompanied by changes in dugong density and a microhabitat shift (i.e. to test for an exchange of food for safety and thereby challenge the predation risk sensitivity hypothesis); and (4) a full model including shark abundance, its interaction with microhabitat category, and microhabitat to test whether foragers manifested a threat-sensitive shift but nevertheless maintained an overall microhabitat preference. In our study area, sea surface temperature (T) covaries with shark abundance (Heithaus 2001b). Consequently, we also evaluated four secondary models, each replacing shark abundance with temperature (i.e. T , $T+M$, $T+M*T$ and $T+M*T+M$), to ensure that statistical relationships between predator abundance and forager microhabitat use were valid and not a spurious result of correlation between shark numbers and temperature. The dependent variable for the models, daily forager counts divided by the relative area of edge and interior microhabitat surveyed, consisted of non-negative values with a mode of zero, a low mean and large variance. Thus, we fit the models using maximum likelihood under the assumption of a negative binomial error distribution (White & Bennetts 1996). We used Akaike's information criteria corrected for small sample size (AIC_c ; Burnham & Anderson 1998; Anderson et al. 2000) to evaluate the strength of each model, and employed Akaike weights (w), which index the likelihood that a model is best among a set of competitors, and the change in AIC_c between models (ΔAIC_c) to assess model uncertainty (Burnham & Anderson 1998). Coefficient estimates with 95% confidence intervals indexed the predictive strengths of individual explanatory variables (Burnham & Anderson 1998).

RESULTS

We sighted 105 foraging dugongs while conducting transects through the seven survey zones; 64 individuals were found in edge microhabitat and 41 were found in interior microhabitat. Most encounters involved solitary animals (53/75), and mean \pm SD group size was 1.40 ± 0.81 , facilitating robust estimation of daily densities for survey zones and across microhabitats. The best model of foraging dugong density incorporated large tiger shark abundance (S) and the interaction between shark abundance and microhabitat ($M*S$; Table 1). This model's Akaike weight (0.80) suggested that it was likely to be superior to its competitors (Table 1). Moreover, the 95% confidence intervals for the coefficient estimates of shark abundance (13.09, 34.56) and its interaction with microhabitat (-22.77 , -43.39) did not encompass zero, suggesting that the relationships between these variables and forager density were statistically significant. The shark abundance variable was associated with a positive coefficient estimate, indicating that, overall, foraging dugong density increased with shark numbers. However, the inclusion of the interaction between shark abundance and microhabitat in the best model means that the manner in which forager densities and predator abundance were related differed as a function of microhabitat: forager densities in edge microhabitats

Table 1. Competing models of the density of foraging dugongs per hectare across two microhabitats (edge and interior) within shallow seagrass patches

Model	K	Δ	w	R^2_c
$S+M*S$	3	0.000	0.799	0.094
$S+M*S+M$	4	3.137	0.166	0.091
$S+M$	3	7.300	0.021	0.078
$T+M*T$	3	9.580	0.007	0.073
$T+M$	3	10.348	0.005	0.072
$T+M*T+M$	4	11.131	0.003	0.074
S	2	30.017	0.000	0.025
T	2	37.271	0.000	0.010
Constant	1	39.785	0.000	—

Forager densities for microhabitats were expressed as counts within survey zones ($N = 7$), divided by the respective area covered by each microhabitat. Independent variables are microhabitat (M), an estimate of large (>3 m) tiger shark abundance (S), sea surface temperature ($^{\circ}C$) (T), the interaction between microhabitat and shark abundance ($M*S$), and the interaction between microhabitat and water temperature ($M*T$). Models were ranked using Akaike's information criterion, corrected for small sample size (AIC_c). For each model, K is the number of parameters in the model +1, Δ is the change in AIC_c between the model and the 'best' model (i.e. the model with the lowest AIC_c ; highlighted in bold), w is the Akaike weight (i.e. the likelihood of preeminence), and R^2_c is the R^2 analogue for models analysed using maximum likelihood.

increased dramatically when shark numbers were elevated, whereas forager densities in interior microhabitats reached minimal levels during periods of peak shark abundance (Fig. 2). On days when foragers were sighted ($N = 53$), the extent to which their use of edge microhabitat exceeded that predicted by food supply was positively correlated with tiger shark abundance (linear regression: $r^2 = 0.15$, $t_{52} = 3.01$, $\beta = 0.42$, $P = 0.004$; Fig. 3). When shark abundance was at its lowest, foragers overused (i.e. selected) interior microhabitats (Fig. 3).

DISCUSSION

Our results are consistent with the hypothesis that microhabitat use by dugongs foraging over seagrass meadows is influenced by the danger of predation. Foraging dugong densities were not equivalent in edge and interior microhabitats throughout the year (rejecting the food quantity hypothesis), nor did foragers consistently overuse meadow interiors (rejecting the food quality hypothesis). Instead, the degree of dissimilarity between forager densities in edge and interior microhabitats was a function of large tiger shark abundance: foraging dugongs underused edge (safe) microhabitat when sharks were scarce and overused edge microhabitat when sharks were common. Moreover, foragers responded to daily changes in shark abundance in a threat-sensitive manner (e.g. Helfman 1989), showing the greatest preference for edge microhabitat when shark abundance was highest. Thus, we surmise that dugongs are sensitive to variation in predation risk across microhabitats within feeding patches, and that individuals manage their probability of death by allocating time to safe but lower-quality feeding microhabitats in proportion to the likelihood of encountering predators.

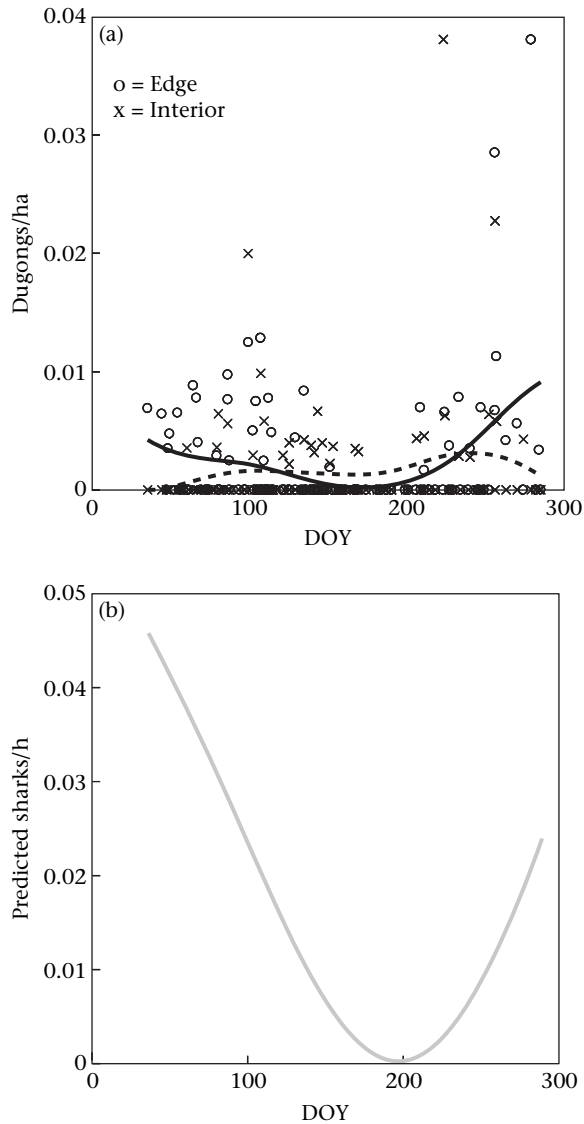


Figure 2. Relation between (a) daily estimates of foraging dugong density (dugongs/ha) in edge (solid black line) and interior (dashed black line) microhabitats within shallow seagrass patches and day of year (DOY) and (b) predicted large (>3 m) tiger shark catch rate (sharks/h; solid grey line) and DOY. Trend lines were generated using distance-weighted least-squares smoothing (DWLS, tension 1.0).

Overall, densities of foraging dugongs in shallow seagrass patches fluctuated with changes in tiger shark abundance. Does this trend indicate that individual dugongs altered their foraging effort in response to changes in predation danger? The results of a companion analysis based on focal animal follows, which show that individual foraging times in the study area were temporally consistent (Wirsing et al., in press b), suggest that the answer is no. Rather, it reflects the fact that fewer dugongs tended to use our study area at times of the year when sharks were scarce (Wirsing et al., in press a). Consequently, densities of foraging dugongs in shallow patches declined in accord with reductions in shark abundance even though individual foraging effort remained constant.

When foraging over shallow seagrass meadows, tiger sharks show a consistent preference for edge microhabitats, putatively in an attempt to match the combined distribution of several of their major prey species (Heithaus 2001a; Heithaus et al. 2006). Consequently, dugongs foraging in edge microhabitats are more likely to encounter sharks than are those feeding in meadow interiors. Yet, individual dugongs increased their use of edge, instead of interior, microhabitats in response to elevated shark abundance. Thus, under the assumption that attack probabilities following an encounter are equal across the two microhabitat categories, we conclude that foraging dugongs assess a microhabitat's danger based primarily on the availability of escape routes into deep (refuge) habitat rather than on predator encounter rates (i.e. predator density). Bottlenose dolphins (*Tursiops* sp.) in our study area also select foraging microhabitats within seagrass meadows that facilitate escape to deep habitat, rather than those with the lowest predator density, during periods of heightened danger from tiger sharks (Heithaus & Dill 2006). For both species, then, we can surmise that the benefit of a nearby refuge (deep water) outweighs the cost of more frequent confrontations with predators in particular seagrass microhabitats, and/or that the availability of escape options at foraging sites is more easily assessed than is the likelihood of future predator encounters (Sih 1992). Such may be the case for many prey animals foraging in habitats where access to refuges varies across fine spatial scales (i.e. between microhabitats; e.g. Grubb & Greenwald 1982; Kotler et al. 1991). In contrast, we would expect prey species that forage in habitats where refuges are either absent or equally accessible across space to rely on predator encounter rates as a measure of danger in particular microhabitats.

Large tiger sharks were most abundant when dugong numbers in our study area were highest. Thus, the predator-induced pattern of microhabitat use reported here may have instead been the result of territorial behaviour if individuals were excluded from preferred interior feeding sites during periods of high dugong density. We consider this scenario to be unlikely, however, given that territorial behaviour has not been observed in our study area, and that dugongs aggregate freely at feeding sites within seagrass patches (Marsh et al. 1984; Preen 1995). Moreover, foraging dugongs adjusted their use of edge and interior microhabitats on a continuous basis, responding to changes in predator abundance even during periods of low dugong density, when the potential influence of territoriality would have been negligible. We also dismiss the possibility that the observed microhabitat shifts were driven by thermoregulatory requirements (i.e. the need to forage in high-quality microhabitats during the cold season, when shark abundance is low, to meet increased metabolic costs). The addition of daily temperature information failed to improve upon predictive models of dugong density in the two microhabitats based solely on shark abundance, and relative use of the microhabitats was extremely sensitive to changes in shark abundance even during warm months when the cost of thermoregulation presumably was low (i.e. between February and April, when sea surface temperatures

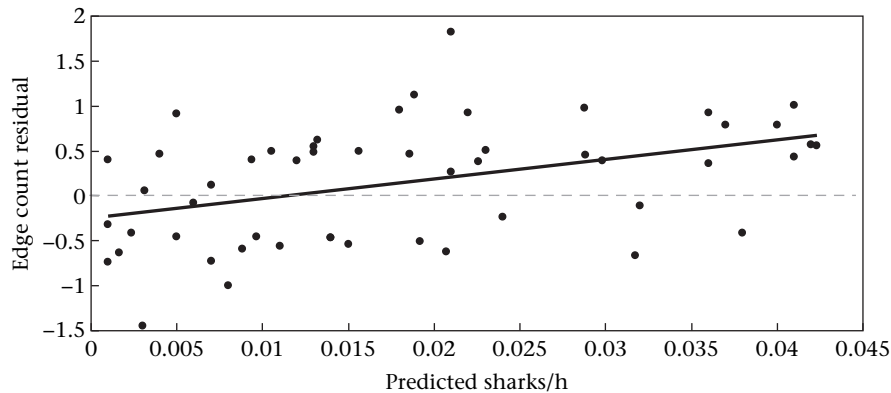


Figure 3. Residual counts of foragers in edge microhabitat (observed counts – expected counts based on food supply; i.e. the proportion of total area within a survey zone defined as edge) versus daily values for large tiger shark catch rate (sharks/h). Equality between observed and expected edge counts (i.e. residual values equalling zero; dashed line) signifies proportional microhabitat use by foragers relative to food (input matching), positive residual values signify overuse of edge microhabitat, and negative residual values signify overuse of interior microhabitat.

consistently exceed 22°C). Finally, although sirenians are known to respond strongly to human disturbance in some situations (e.g. Nowacek et al. 2004), we can reject the possibility that vessel traffic drove or contributed to the microhabitat shifts that we observed. Use of the study area by boats is light, temporally consistent and spatially dispersed, so interactions with boats would not be expected to elicit fine-scale changes in the use of edge and interior feeding sites by dugongs.

The tendency of foraging dugongs to select interior microhabitats during periods of low predation danger, rather than to input-match, can be explained by the depressed nutrient (organic carbon) content of *A. antarctica* plants growing along the edges of the seagrass patches used in this study (Heithaus et al., in press). However, it is also possible that dugongs foraged preferentially in interior microhabitats during safe periods in part (1) to avoid paying energetic costs associated with diving more deeply to access seagrass growing in edge microhabitats, and/or (2) because tropical seagrass species not included in our food biomass estimates are less available in edge microhabitats. The latter alternative is unlikely, given that a disparity in tropical seagrass biomass between edge and interior microhabitats is not known to exist, and that the overall availability of these species in our study area tends to be extremely low when tiger sharks are scarce (i.e. June–August) (Walker & McComb 1988; Walker et al. 1988).

In a companion study, we found that the danger of tiger shark predation affects the use of shallow and deep habitats by foraging dugongs, with individuals overusing deep but impoverished refuges when large shark abundance is elevated (Wirsing et al., in press a). The present investigation reveals that dugongs also adjust their use of safe but energy-poor microhabitats while feeding in accord with changes in predation danger. Collectively, these results indicate that the threat of tiger shark attack can influence not only use of profitable but dangerous feeding patches by large marine herbivores (i.e. broad-scale habitat selection, in this case on the order of hundreds of metres to kilometres), but also choice of feeding sites within these foraging patches (i.e. fine-scale habitat selection, in this

case on the order of tens of metres). Grazing by dugongs can dramatically alter seagrass biomass and patch composition, especially where foraging pressure is heavy (i.e. at high-quality feeding sites within patches; de Jongh et al. 1995; Preen 1995; Nakaoka & Aioi 1999; Masini et al. 2001). Therefore, by altering the use of foraging microhabitats by dugongs, tiger sharks may exert powerful indirect effects on seagrass, alleviating pressure experienced by plants growing at preferred but dangerous feeding sites (e.g. interiors) and augmenting pressure experienced by nutritionally inferior plants growing at relatively safe feeding sites (e.g. edges). By implication, changes in patterns of large shark abundance and space use where dugongs, as well as other large marine herbivores (e.g. sea turtles; Heithaus et al., in press), occur may trigger behaviourally mediated trophic cascades (BMII; see Dill et al. 2003), with profound consequences for the microhabitat structure of seagrass patches and, ultimately, benthic communities.

Dugongs are large bodied, long-lived animals that suffer low predation rates (Marsh et al. 1984). Consequently, their relationship with predators has rarely been addressed, and the possibility that predators affect their behaviour has even been dismissed (e.g. Anderson 1982). Yet, using an analytical approach (assessment of consumer time allocation in relation to spatial and temporal variation in resource availability and predator abundance) that is commonly used in more tractable terrestrial and aquatic environments (Brown & Kotler 2004), we were able to show that dugongs select foraging microhabitats in a manner that facilitates predator evasion and may have community consequences. We conclude, therefore, by encouraging more widespread use of this research tool in marine systems. Future studies invoking it will almost certainly enhance our understanding of, and appreciation for, the sublethal effects of predators on marine consumers, including species believed to be relatively immune to predation pressure. Moreover, such studies are likely to improve our ability both to assess the ecological roles of marine predator and prey species and to predict the effects of changes in their distribution and abundance on community structure.

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References

- Anderson, D. R., Burnham, K. P. & Thompson, W. L. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, **64**, 912–923.
- Anderson, P. K. 1982. Studies of dugongs at Shark Bay, Western Australia. II. Surface and subsurface observations. *Australian Wildlife Research*, **9**, 85–99.
- Anderson, P. K. 1986. Dugongs of Shark Bay, Australia: seasonal migration, water temperature and forage. *National Geographic Research*, **2**, 473–490.
- Anderson, P. K. 1995. Scarring and photoidentification of dugongs (*Dugong dugon*) in Shark Bay, Western Australia. *Aquatic Mammals*, **21**, 205–211.
- van Baalen, M. & Sabelis, M. W. 1993. Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. *American Naturalist*, **142**, 646–670.
- Brown, J. S. 1999. Vigilance, patch use, and habitat selection: foraging under predation risk. *Evolutionary Ecology Research*, **1**, 49–71.
- Brown, J. S. & Kotler, B. P. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, **7**, 999–1014.
- Burnham, K. P. & Anderson, D. R. 1998. *Model Selection and Inference: a Practical Information-theoretic Approach*. New York: Springer-Verlag.
- Chilvers, B. L., Delean, S., Gales, N. J., Holley, D. K., Lawler, I. R., Marsh, H. & Preen, A. R. 2004. Diving behaviour of dugongs, *Dugong dugon*. *Journal of Experimental Marine Biology and Ecology*, **304**, 203–224.
- Crawley, M. J. 1983. *Herbivory*. Los Angeles: University of California Press.
- Danell, K. & Bergström, R. 2002. Mammalian herbivory in terrestrial environments. In: *Plant–Animal Interactions* (Ed. by C. M. Herrera & O. Pellmyr), pp. 107–131. Oxford: Blackwell Scientific.
- Dill, L. M., Heithaus, M. R. & Walters, C. J. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology*, **84**, 1151–1157.
- Fretwell, S. D. & Lucas, H. L., Jr. 1970. On territorial behavior and other factors influencing habitat distributions in birds: I. Theoretical developments. *Acta Biotheoretica*, **19**, 16–36.
- Gales, N., McCauley, R. D., Lanyon, J. & Holley, D. 2004. Change in abundance of dugongs in Shark Bay, Ningaloo and Exmouth Gulf, Western Australia: evidence for large-scale migration. *Wildlife Research*, **31**, 283–290.
- Grubb, T. C. & Greenwald, L. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy-cost. *Animal Behaviour*, **30**, 637–640.
- Heithaus, M. R. 2001a. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. *Oikos*, **92**, 542–554.
- Heithaus, M. R. 2001b. The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet and seasonal changes in catch rates. *Environmental Biology of Fishes*, **61**, 25–36.
- Heithaus, M. R. & Dill, L. M. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, **83**, 480–491.
- Heithaus, M. R. & Dill, L. M. 2006. Does tiger shark predation risk influence dolphin habitat use at multiple spatial scales? *Oikos*, **114**, 257–264.
- Heithaus, M. R., Dill, L. M., Marshall, G. J. & Buhleier, B. M. 2002. Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a subtropical seagrass ecosystem. *Marine Biology*, **140**, 237–248.
- Heithaus, M. R., Hamilton, I. M., Wirsing, A. J. & Dill, L. M. 2006. Validation of a randomization procedure to assess animal habitat preferences: microhabitat use of tiger sharks in a seagrass ecosystem. *Journal of Animal Ecology*, **75**, 666–676.
- Heithaus, M. R., Frid, A., Wirsing, A. J., Dill, L. M., Fourqurean, J. W., Burkholder, D., Thomson, J. & Bejder, L. In press. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal Ecology*.
- Helfman, G. S. 1989. Threat-sensitive predator avoidance in damselfish–trumpetfish interactions. *Behavioural Ecology and Sociobiology*, **24**, 47–58.
- Hugie, D. M. & Dill, L. M. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology, Supplement A*, **45**, 151–169.
- de longh, H. H., Wenno, B. J. & Meelis, E. 1995. Seagrass distribution and seasonal biomass changes in relation to dugong grazing in the Moluccas, East Indonesia. *Aquatic Botany*, **50**, 1–19.
- Johnson, J. B. & Omland, K. S. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101–108.
- Kotler, B. P., Brown, J. S. & Hasson, O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology*, **72**, 2249–2260.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behaviour*, **27**, 215–290.

- Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
- Lowe, C. G., Wetherbee, B. M., Crow, G. L. & Tester, A. L. 1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environmental Biology of Fishes*, **47**, 203–211.
- Luttbeg, B. & Sih, A. 2004. Predator and prey habitat selection games: the effects of how prey balance foraging and predation risk. *Israel Journal of Zoology*, **50**, 233–254.
- Marsh, H., Prince, R. I. T., Saalfeld, W. K. & Shepherd, R. 1994. The distribution and abundance of the dugong in Shark Bay, Western Australia. *Wildlife Research*, **21**, 149–161.
- Marsh, H., Heinsohn, G. E. & Marsh, L. M. 1984. Breeding cycle, life history, and population dynamics of the dugong. *Australian Journal of Zoology*, **32**, 767–788.
- Masini, R. J., Anderson, P. K. & McComb, A. J. 2001. A *Halodule*-dominated community in a subtropical embayment: physical environment, productivity, biomass and impact of dugong grazing. *Aquatic Botany*, **71**, 179–197.
- Nakaoka, M. & Aioi, K. 1999. Growth of the seagrass *Halophila ovalis* at the dugong trails compared to existing within-patch variation in a Thailand intertidal flat. *Marine Ecology Progress Series*, **184**, 97–103.
- Nowacek, S. M., Wells, R. S., Owen, E. C. G., Speakman, T. R., Flamm, R. O. & Nowacek, D. P. 2004. Florida manatees, *Trichechus manatus latirostris*, respond to approaching vessels. *Biological Conservation*, **119**, 517–523.
- Preen, A. 1995. Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. *Marine Ecology Progress Series*, **124**, 201–213.
- Preen, A. R., Marsh, H., Lawler, I. R., Prince, R. I. T. & Shepherd, R. 1997. Distribution and abundance of dugongs, turtles, dolphins, and other megafauna in Shark Bay, Ningaloo Reef and Exmouth Gulf, Western Australia. *Wildlife Research*, **24**, 185–208.
- Schmitz, O. J., Krivan, V. & Ovadia, O. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, **7**, 153–163.
- Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In: *Predation: Direct and Indirect Impacts on Aquatic Communities* (Ed. by W. C. Kerfoot & A. Sih), pp. 203–224. Hanover, New Hampshire: University Press of New England.
- Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *American Naturalist*, **139**, 1052–1069.
- Walker, D. I. & McComb, A. J. 1988. Seasonal variation in the production, biomass and nutrient status of *Amphibolis antarctica* (Labill.) Sonder Ex Aschers. and *Posidonia australis* Hook. F. in Shark Bay, Western Australia. *Aquatic Botany*, **31**, 259–275.
- Walker, D. I., Kendrick, G. A. & McComb, A. J. 1988. The distribution of seagrass species in Shark Bay, Western Australia, with notes on their ecology. *Aquatic Botany*, **30**, 305–317.
- White, G. C. & Bennetts, R. E. 1996. Analysis of frequency count data using the negative binomial distribution. *Ecology*, **77**, 2549–2557.
- Wirsing, A. J., Heithaus, M. R. & Dill, L. M. 2006. Tiger shark (*Galeocerdo cuvier*) abundance and growth rates in a subtropical embayment: evidence from seven years of standardized fishing effort. *Marine Biology*, **149**, 961–968.
- Wirsing, A. J., Heithaus, M. R. & Dill, L. M. In press a. Fear factor: do dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)? *Oecologia*.
- Wirsing, A. J., Heithaus, M. R. & Dill, L. M. In press b. Can you dig it? Use of excavation, a risky foraging tactic, by dugongs is sensitive to predation danger. *Animal Behaviour*.