

Predator-induced modifications to diving behavior vary with foraging mode

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Breath-hold divers are strongly interacting species whose top–down influence on aquatic communities is shaped by factors governing their diving decisions. Although some of these factors (e.g. physiological constraints, energetic needs) have been scrutinized, the possibility that predation risk influences diving behavior has been largely overlooked, and no study to date has asked if anti-predator responses by divers depend on foraging mode. We contrasted dive cycle changes by herbivorous dugongs *Dugong dugon* using two foraging tactics – cropping, which always permits anti-predator vigilance, and excavation, which limits surveillance at depth – in response to temporal variation in tiger shark *Galeocerdo cuvier* abundance. Dugongs responded to increasing shark abundance (one component of predation risk) by diving more frequently without changing their surface times and thereby spending a greater proportion of time at the surface, but only while excavating. When threatened, in other words, excavating dugongs sacrificed foraging time at depth to facilitate shark detection. In contrast, cropping dugongs at risk from sharks were able to continue diving and foraging normally. By implication, future studies should consider the influence of predation risk on diving decisions, even by large-bodied species, and the possibility that behavioral responses by divers to predators may vary with foraging mode.

Air-breathing aquatic foragers (e.g. marine mammals and reptiles, diving birds) must balance the need for oxygen recovery at the surface and resource exploitation at depth (Houston and Carbone 1992). Accordingly, their diving behavior is widely assumed to be a product of the interplay between these twin concerns (Kramer 1988, Carbone and Houston 1996, Thompson and Fedak 2001). Yet, most breath-hold divers are also faced with the prospect of becoming a meal themselves, so they may alter their diving behavior in order to mitigate predation risk (Heithaus and Frid 2003). Despite growing theoretical support (Frid et al. 2006, 2007a, 2008, 2009), this possibility has received little empirical evaluation (Frid et al. 2007a, Dunphy-Daly et al. 2010) and continues to be ignored (Frid et al. 2007b). Given that ecological interactions of divers are spatially and temporally structured by their diving decisions (Boyd 1997) and that divers are often species whose absence or rarity can lead to ecosystem transformation (i.e. ‘strongly interactive species’, sensu Soulé et al. 2005), studies of diving under predation risk should yield valuable insights about aquatic community dynamics. They will also improve our understanding of the influence that aquatic predators have on populations of their air-breathing prey and community properties by inducing changes in mesoconsumer (i.e. mid-trophic level predator or herbivore) diving behavior. A better understanding of these top–down effects has become vital because many large-bodied

aquatic predators appear to be in worldwide decline (Pauly et al. 1998, Myers and Worm 2003).

The risk of predation experienced by prey individuals can vary with foraging mode (Bednekoff and Lima 1998, Kaby and Lind 2003, Guillemain et al. 2007). For example, foraging tactics that are complex (Kaby and Lind 2003) or obstruct vision (Krause and Godin 1996) are more likely to impede detection and escape from predators than those that facilitate surveillance. Consequently, individuals using inherently dangerous foraging modes may be especially responsive to the presence of predators and compensate by investing more heavily in other forms of anti-predator behavior (e.g. avoidance, altered activity patterns). Among aquatic air breathers, for instance, we might expect individuals employing risky foraging tactics to dive in a manner that confers greater protection from predators than conspecifics using safer feeding modes. Here, we present an unprecedented test of this hypothesis using diving dugongs *Dugong dugon* foraging under temporally variable threat of predation by tiger sharks *Galeocerdo cuvier* in the subtropical seagrass ecosystem of Shark Bay, Australia.

Dugongs forage either by stripping clusters of leaves from the branching stems of seagrass plants (cropping) or by removing entire seagrass plants from the substrate to consume both leaves and rhizomes (excavation) (Aragones et al. 2006, Wirsing et al. 2007a). Excavation is likely more

profitable because it enables dugongs to add important nutrients that are plentiful in rhizomes (e.g. organic carbon) to the high concentrations of nitrogen found in seagrass leaves (Marsh et al. 1982, de Iongh et al. 1995). However, this tactic also involves extended periods of digging, during which time vigilance is compromised, and creates huge sediment plumes that further obscure visibility and may actually draw the attention of predators. Conversely, the cropping tactic is presumably less profitable but does not cloud the water and allows for frequent visual scans between bites. Thus, dugongs engaged in excavation likely pay the cost of increased predation risk from tiger sharks, which are able to detect prey in murky water through mechano- (lateral line system) and/or electroreception (Wirsing et al. 2007a). The magnitude of this cost in Shark Bay changes over time, however, because tiger shark abundance in the bay fluctuates between a high in February and a low in July each year (Wirsing et al. 2006). Under the assumption that diving by dugongs is sensitive to the threat posed by tiger sharks, we predicted that excavating dugongs would respond to rising shark abundance (i.e. increasing probability of predator encounters and therefore need for anti-predator investment) with compensatory adjustments to their diving behavior to a greater extent than those foraging with the cropping tactic. In Shark Bay, foraging dugongs that detect the approach of a shark are able to flee from shallow seagrass banks into deeper waters that offer little food but allow for increased maneuverability and, consequently, a higher chance of surviving an attack (Wirsing et al. 2007b). Thus, dugongs in the act of excavation are presumably at greatest risk from sharks when they are digging seagrass plants up from the substrate, and their vision is obscured by suspended sediment, and safest while breathing at the surface, where they expose only their rostrum to the air and are able to continuously scan their surroundings. Accordingly, we expected excavating dugongs to compensate for increasing shark abundance by making more frequent trips to the surface (i.e. by spending a reduced portion of their time digging for seagrass rhizomes at depth).

Material and methods

Study site

This study was conducted over the course of four years (2002–2004, 2006) in the Eastern Gulf of Shark Bay, offshore of the Monkey Mia Dolphin Resort (~25°45'S, 113°44'E). The Shark Bay region is protected as a World Heritage Area and is occupied by 10 000–14 000 dugongs (Gales et al. 2004), many of which forage in our study area (Wirsing et al. 2007b). The dugong's only known predator in the area is the tiger shark.

Predator abundance

Catch rates provide a reliable measure of tiger shark abundance in Shark Bay (Heithaus 2001, Wirsing et al. 2006). Over the course of the four-year study, we caught tiger sharks ($n = 211$) on single-hook drumlines baited primarily with Australian salmon *Arripis truttaceus* and deployed between dawn and dusk in six fishing zones throughout the study area

(~160 km²) (Wirsing et al. 2006, Wirsing et al. unpubl.). Although our sampling effort was intensive, we did not fish for sharks every day. Thus, we fit our catch rate data with a sinusoidal function using maximum likelihood (Wirsing et al. 2007b). This modeling procedure, which used a period of one year and assumed a Poisson error distribution because our data consisted of integer values for the number of sharks caught per day, allowed us to predict the annual trend in daily shark catch rates and, as a result, furnished a robust estimate of relative tiger shark abundance for each day of the year (years pooled). Because tiger sharks under 3.0 m in length (TL) are unlikely to pose a threat to adult dugongs (Wirsing et al. 2007b), only sharks larger than this were used to estimate daily abundance ($n = 78$). However, the inclusion of smaller tiger sharks does not change the results presented below. Although absolute tiger shark abundance in our study area varies with habitat, being consistently higher over shallow banks than in deeper areas (Heithaus et al. 2006), the annual trend in shark abundance does not.

Dugong diving behavior

We assessed the diving behavior of individual dugongs using focal animal follows ($n = 56$; Altmann 1974) conducted between January and May, an interval during which both foraging tactics are used (Wirsing et al. 2007a) and tiger shark abundance drops from its peak to relatively low levels (Wirsing et al. 2006). Individual adults sighted randomly along transect passes over shallow seagrass banks (see Wirsing et al. 2007b for detailed transect methods) were chosen for focal observation, reducing the possibility that starting positions were spatially biased (Heithaus et al. 2006). Follows were only conducted in Beaufort wind conditions ≤ 1 to ensure that our observations were reliable. Focal animals were approached at slow speed (~1 km h⁻¹) and then allowed to acclimate to our vessel (a 4.5 m runabout) for 5 min from a distance of roughly 50 m; behavioral observations were then made from a distance of 10–20 m. This method of observation is minimally invasive: focal individuals almost never altered their behavior or moved in response to our approach and moved freely about the vessel, suggesting that we were not perceived as a distraction or a threat. Dugongs that did change their behavior or move as we approached ($n = 5$) were not followed.

During each follow, we recorded water depth (m) and the focal individual's position (with a GPS), dominant behavioral state (foraging or not), and dominant foraging mode (excavation or cropping) every two minutes. Behavioral states and foraging modes were usually determined via direct observation of the submerged animal or, when sub-surface activity could not be seen, using diagnostic behavior and characteristics at the surface (Chilvers et al. 2004): foraging dugongs can be distinguished from those that are resting or travelling based on their slow pace, irregular surface intervals, and tendency to bring more of the body out of the water in preparation for a deeper dive, while cropping dugongs can be differentiated from excavating individuals based on their meandering search paths and the absence of a sediment plume (note that cropping was never inferred solely from the absence of a plume). We also recorded the timing of every breath, allowing us to calculate the total number of dives made by each focal dugong and

the duration of each of its surface and submerged intervals. For the purposes of this study, we considered a follow to be over when the focal individual left shallow seagrass bank habitat (depths ≤ 4.5 m) for deeper water. The water depth range over which follows were undertaken was 1.5–4.5 m, and individual focal dugongs remained at relatively constant water depths during follows (mean depth range per follow = 1.06 m, \pm SD = 0.92 m). During follows we noted unique scars and markings to ensure that no individual was observed more than once, and restricted our analysis to follows that featured at least 20 min of continuous foraging activity. Focal observation periods subjected to analysis averaged 41.1 min (\pm SD = 18.6 min).

Statistical analysis

We considered a dive cycle to consist of a dive (submerged) interval and the post-dive surface interval; the number of dive cycles recorded during follows ranged from 13 to 56. We analyzed four dive cycle parameters that could change in response to variation in predation risk: (1) mean time spent at the surface (i.e. average surface interval duration, TAS); (2) mean time spent at depth (i.e. average submerged interval duration, TAD); (3) diving rate (dives per hour); and (4) mean dive-pause ratio (i.e. the ratio of submerged time to surface time, DPR). Though correlated, these dive cycle components were analyzed as separate dependent variables so that we could identify which ones, if any, were responsive to predation danger. For all four dependent variables, each focal dugong contributed a single mean value ($n = 38$ cropping individuals; $n = 18$ excavating individuals). Data for time at the surface, time at depth, and dive-pause ratio were normalized using log transformations (Shapiro-Wilks test: TAS, $W = 0.965$, $p = 0.104$; TAD, $W = 0.987$, $p = 0.816$; DPR, $W = 0.966$, $p = 0.115$) and then fit using general linear models, while data for diving rate were modeled using Poisson regression with a log link function. Explanatory variables included in all models were foraging tactic (cropping or excavation), relative tiger shark abundance (estimated sharks caught h^{-1}), mean water depth (to account for differences in travel time to and from the bottom), and year (2002–2004, 2006). We also always included the interaction between foraging tactic and shark abundance to test for divergent diving behavior by cropping and excavating dugongs in response to changing predation risk; other possible interactions were excluded from final models if they were non-significant. Effects of explanatory variables were deemed significant if their 95% confidence interval did not overlap zero (Johnson 1999).

In Shark Bay, tiger shark abundance and ocean temperature covary positively (Heithaus 2001). Thus, we needed to ensure that any observed statistical links between changing shark abundance and dugong dive cycle features were not confounded by an underlying relationship between dugong diving and water temperature. Accordingly, because strong multicollinearity precluded the inclusion of these two variables in the same model, we built competing models of each of the four dependent variables in which estimates of tiger shark abundance were replaced with measures of water temperature (taken during each follow). We compared the fit of shark- and temperature-based models of each dependent

variable using Akaike's information criterion, corrected for small sample size (AIC_c , Burnham and Anderson 2002). In performing these non-nested model comparisons, we took superiority of the shark-based model (lower AIC_c) to mean that observed statistical relationships between predation risk and diving behavior were not confounded by an underlying influence of water temperature.

To graphically depict modeled relationships between tiger shark abundance and the four diving metrics, we generated partial regression plots (Belsley et al. 2004). These plots feature residuals from regressing the dependent variable against all explanatory variables, save the one of interest, on the y-axis and residuals from regressing the explanatory variable of interest against the remaining explanatory variables on the x-axis. As such, they isolate the role of particular explanatory variables within multiple regression models. That is, slopes of partial regression plots show the effect of one explanatory variable (in this case shark abundance) on the dependent variable (in this case TAS, TAD, diving rate, or DPR) after controlling for its multicollinearity with, and the effects of, other explanatory variables. For each diving metric, partial regression plots distinguish between residuals and slopes for cropping and excavating dugongs and thereby illustrate any differences in the responses of individuals using these two tactics to changing shark abundance.

Results

Time at surface (TAS)

Overall, time spent at the surface per dive cycle by dugongs foraging over shallow seagrass banks averaged 2.79 (± 0.85 , SD) seconds and did differ significantly as a function of foraging tactic (cropping, mean = 2.98 \pm 0.93 s; excavating, mean = 2.40 \pm 0.45 s), tiger shark abundance, water depth, year, and the interaction between foraging tactic and shark abundance (Table 1, Fig. 1a). Replacement of shark abundance with water temperature produced a final model of TAS with nearly identical support ($\Delta AIC_c = +0.002$).

Table 1. General linear model of mean time at surface (TAS) per dive cycle for foraging dugongs ($n = 56$) in Shark Bay, Western Australia. A log transformation was used to normalize the dependent variable. Explanatory variables included in the final model are water depth (depth), foraging tactic (cropping versus excavation), tiger shark abundance (shark), year (2002–2004, 2006), and the interaction of tiger shark abundance and foraging tactic (shark \times foraging tactic); other possible interactions were all non-significant (95% CI overlapping zero) and therefore excluded (and note that the model is unchanged if the non-significant shark \times foraging tactic term is removed).

Parameter	β	95% CI
Intercept	0.381	0.196, 0.565
Depth	0.020	-0.014, 0.054
Foraging tactic	-0.053	-0.239, 0.133
Shark	0.179	-3.730, 4.089
Shark \times Foraging tactic	0.026	-6.939, 6.992
Year (2002)	0.024	-0.111, 0.160
Year (2003)	0.027	-0.080, 0.135
Year (2004)	0.014	-0.067, 0.094
Year (2006)	-	-

Significant relationships appear in bold.

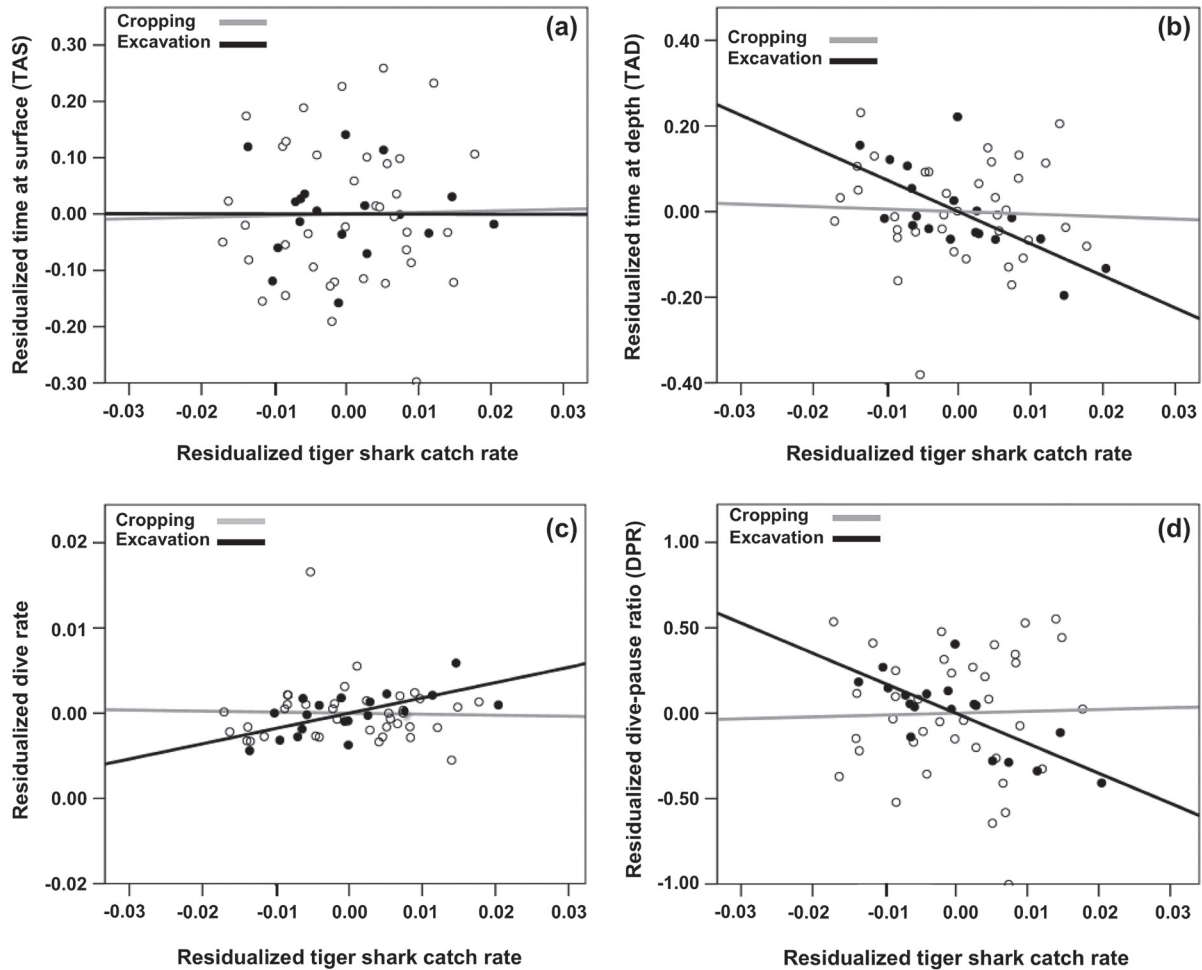


Figure 1. Partial regression plots of residuals from regressing (a) time at surface (TAS), (b) time at depth (TAD), (c) diving rate, and (d) dive-pause ratio (DPR) for diving dugongs against all explanatory variables save estimated tiger shark abundance (i.e. ‘Residualized’ values for the dependent variables, y-axis) and residuals from regressing estimated tiger shark abundance against the remaining explanatory variables (‘Residualized tiger shark catch rate’, x-axis). Slopes show the effect of shark abundance on each dependent variable after controlling for multicollinearity with, and the effects of, the other explanatory variables. Residuals and slopes are depicted separately for cropping (open circles, gray line) and excavating (black circles, black line) dugongs to illustrate differential responses to changing shark numbers.

Time at depth (TAD)

Time at depth per dive cycle averaged $93.34 (\pm 36.40, \text{SD})$ seconds overall and did not differ significantly with respect to foraging tactic (cropping, mean = 100.32 ± 37.76 s; excavating, mean = 78.62 ± 29.07 s), shark abundance, and year (Table 2). However, TAD did increase significantly with water depth (Table 2), and was also influenced by the interaction between foraging tactic and shark abundance: TAD was inversely related to shark abundance among excavating but not cropping dugongs (Table 2, Fig. 1b). Replacement of shark abundance with water temperature yielded a final model of TAD with somewhat weaker support ($\Delta\text{AIC}_c = +2.26$).

Diving rate

The rate of diving by foraging dugongs was influenced only by water depth and the interaction of foraging tactic and shark abundance (Table 3): dugongs made fewer dives as depth increased and only excavating dugongs increased their diving rate along with rising shark abundance (Fig. 1c).

The temperature-based model of diving rate was inferior to the shark-based model ($\Delta\text{AIC}_c = +2.24$).

Dive-pause ratio (DPR)

The dive-pause ratio characterizing foraging dugongs varied significantly as a function of water depth and the interaction between foraging tactic and shark abundance (Table 4): the proportion of the dive cycle that dugongs allocated to the post-dive surface interval decreased with increasing depth and only excavating dugongs spent relatively more time at the surface compared to time spent beneath it (i.e. decreased their DPRs) as tiger shark abundance increased (Fig. 1d). Replacement of shark abundance with temperature resulted in a model of DPR with less support ($\Delta\text{AIC}_c = +1.75$).

Discussion

The influence of predation risk on diving by air-breathing aquatic foragers has a strong theoretical basis (Frid et al.

Table 2. General linear model of mean time at depth (i.e. submerged, TAD) per dive cycle for foraging dugongs. A log transformation was used to normalize the dependent variable. Explanatory variables included in the final model are water depth (depth), foraging tactic (cropping versus excavation), tiger shark abundance (shark), year (2002–2004, 2006), and the interaction of tiger shark abundance and foraging tactic (shark × foraging tactic); other possible interactions were all non-significant (95% CI overlapping zero) and therefore excluded.

Parameter	β	95% CI
Intercept	1.679	1.511, 1.847
Depth	0.106	0.076, 0.137
Foraging tactic	0.152	-0.018, 0.321
Shark	-0.449	-4.016, 3.118
Shark × Foraging tactic	-7.389	-13.745, -1.034
Year (2002)	0.011	-0.113, 0.135
Year (2003)	0.000	-0.099, 0.097
Year (2004)	0.060	-0.014, 0.134
Year (2006)	–	–

Significant relationships appear in bold.

2007b). Moreover, a number of studies have inferred that certain aspects of diving behavior may have been shaped by predation danger (e.g. nocturnal deep diving and scanning prior to surfacing by sea turtles; Hayes et al. 2001, Houghton et al. 2008). Yet, the impact of predators on diving decisions has received scant empirical attention, and changes in diving behavior triggered by varying predation risk have only rarely been demonstrated (Dunphy-Daly et al. 2010). Here, we provide the best field demonstration to date that the threat of predation can induce breath-hold divers to adjust the parameters of their dive cycles. Moreover, for the first time, we show that anti-predator alterations made by individual divers are contingent upon their foraging mode. In accord with our prediction, dugongs over shallow seagrass meadows responded to an increasing threat of tiger shark predation by diving more frequently without changing their surface times and thereby spending a smaller proportion of each dive cycle at depth, but only when using a foraging tactic – excavation – that constrains anti-predator vigilance more at the ocean bottom than at the surface. Our results add to

Table 3. Generalized linear model of foraging dugong dive rate (number of dives per hour) as a function of water depth (depth), foraging tactic (cropping versus excavation), tiger shark abundance (shark), year (2002–2004, 2006), and the interaction of tiger shark abundance and foraging tactic (shark × foraging tactic); other possible interactions were all non-significant (95% CI overlapping zero) and not included in the final model. A Poisson error distribution served as the basis for statistical inference.

Parameter	β	95% CI
Intercept	0.491	0.147, 0.835
Depth	-0.197	-0.265, -0.129
Foraging tactic	-0.299	-0.616, 0.018
Shark	-6.704	-14.318, 0.911
Shark × Foraging tactic	24.880	13.829, 35.932
Year (2002)	-0.264	-0.537, 0.010
Year (2003)	0.124	-0.060, 0.308
Year (2004)	-0.166	-0.299, -0.032
Year (2006)	–	–

Significant relationships appear in bold.

Table 4. General linear model of mean dive-pause ratio (i.e., surface time divided by dive time, DPR) per dive cycle for foraging dugongs. A log transformation was used to normalize the dependent variable. Explanatory variables included in the final model are water depth (depth), foraging tactic (cropping versus excavation), tiger shark abundance (shark), year (2002–2004, 2006), and the interaction of tiger shark abundance and foraging tactic (shark × foraging tactic); other possible interactions were all non-significant (95% CI overlapping zero) and therefore excluded.

Parameter	β	95% CI
Intercept	1.356	0.851, 1.861
Depth	0.086	0.041, 0.131
Foraging tactic	1.345	-0.851, 3.542
Shark	1.624	-9.092, 12.329
Shark × Foraging tactic	-20.554	-39.647, -1.461
Year (2002)	-0.005	-0.186, 0.176
Year (2003)	0.129	-0.165, 0.423
Year (2004)	-0.129	-0.350, 0.092
Year (2006)	–	–

Significant relationships appear in bold.

existing theoretical arguments (Heithaus and Frid 2003, Frid et al. 2007b) that failure to account for predation risk may lead to flawed assessments of diving behavior and, ultimately, the role of divers in ecological communities.

Many air-breathing divers employ more than one foraging tactic, including cetaceans (e.g. Indian Ocean bottlenose dolphins *Tursiops aduncus*, Sargeant et al. 2007, Sargeant and Mann 2009), pinnipeds (e.g. harbour seals *Phoca vitulina*, Bowen et al. 2002), sea otters (e.g. California sea otter *Enhydra lutris nereis*, Tinker et al. 2008), marine birds (e.g. great cormorants *Phalacrocorax carbo* and European shags *Phalacrocorax aristoteli* Grémillet et al. 1998), and marine reptiles (e.g. green sea turtles *Chelonia mydas*, Heithaus et al. 2002). Our findings reveal that the strength and nature of diving responses of these species to predation risk may depend on their foraging mode, especially in cases where certain tactics are particularly likely to inhibit vigilance (e.g. bottom-grubbing in Indian Ocean bottlenose dolphins, Sargeant et al. 2007; benthic digging by cormorants, Grémillet et al. 1998). By implication, studies failing to consider the possibility of interaction between foraging behavioral polymorphism and threat-sensitivity in any particular breath-hold diver risk overlooking dive cycle adjustments triggered by exposure to predators and, therefore, drawing erroneous conclusions about the factors shaping diving decisions. Had we not differentiated between cropping and excavating individuals, for example, we would have concluded that tiger sharks exert little or no influence on the diving behavior of dugongs foraging over seagrass meadows.

Most studies to date have explored the influence of predation risk on a single prey behavior (Relyea 2001, Lind and Cresswell 2005). Yet, when exposed to the threat of tiger shark predation, dugongs in Shark Bay respond with a suite of behavioral adjustments: they increase their use of low profitability deep channels where sharks are less numerous and easier to evade (Wirsing et al. 2007b), shift their foraging activity to the periphery of seagrass meadows where escape into deep water is facilitated (Wirsing et al. 2007c), and decrease their reliance on excavation, which

constrains vigilance (Wirsing et al. 2007a). By adding yet another dimension to the anti-predator behavior of dugongs – dive cycle alteration while excavating – the results of the present investigation help put to rest the notion that, like many long-lived marine mammals, dugongs are not subject to the effects of predation risk (Heithaus et al. 2008, Wirsing et al. 2008) and, more importantly, highlight the myriad ways in which predators can alter the behavior of their prey. Therefore, future studies that account for the possibility of anti-predator behavioral diversity should greatly improve our understanding of the influence of predators on individual fitness, prey populations, and community properties.

Diving adjustments by excavating dugongs under risk from sharks have potentially important implications for the composition of coastal seagrass meadows. Excavation foraging by dugongs disrupts seagrass meadow structure, creating furrows and open patches that promote succession (de Jongh et al. 1995, Preen 1995, Masini et al. 2001), while cropping does not. Thus, by inducing excavating dugongs to spend less time foraging at depth (i.e. more time at the surface scanning for predators), tiger sharks may indirectly reduce the magnitude of physical disturbance experienced by seagrass beds during periods when they are present and, as a result, inhibit colonization by fast-growing pioneering species while facilitating slow-growing competitive dominants (e.g. *Amphibolis antarctica* in Shark Bay). In Shark Bay and other areas where dugongs and large sharks co-occur, studies contrasting the diving profiles of and the disturbance to seagrass meadows caused by excavating dugongs during periods of low and high shark abundance should help to reveal whether predator-induced adjustments to the dugong dive cycle are sufficient to trigger this possible indirect effect in plant communities.

Previous models of diving under the risk of predation assumed that divers would alter both their time at the surface (TAS) and time at depth (TAD) per dive cycle in order to manage their risk of predation and optimize time at foraging depths (Heithaus and Frid 2003), yet we only documented a reduction in TAD driven by increased diving rate when tiger sharks were abundant. This inconsistency likely owes its existence to the fact that the mean surface time we recorded for excavating dugongs (2.40 s) approaches the minimum observed for diving dugongs (Churchward 2001, Chilvers et al. 2004). With little scope to further reduce their TAS, in other words, the excavating dugongs we followed could only surface more frequently in order to mitigate their risk of tiger shark predation (i.e. spend more, shorter periods inside plumes of sediment than would optimize time at the bottom foraging), producing shorter dive cycles without any change in the surface interval.

Positive correlation between shark abundance and water temperature in Shark Bay (Heithaus 2001) gives rise to the possibility that the link between dugong diving and predation risk reported here is an artifact of an underlying relationship between the dugong dive cycle and thermoregulatory costs. We suggest, however, that changes in water temperature did not strongly influence the diving behavior we observed for two reasons. First, the imposition of any thermoregulatory costs accompanying drops in ambient temperature would have been expected to alter

the diving behavior of dugongs using both foraging tactics, yet only excavating individuals manifested increased TAD when water temperatures (and shark abundance) were relatively low. Second, shark-based final models of the three dive cycle parameters that varied over the course of the investigation among excavating dugongs (TAD, diving rate, DPR) were consistently superior to their temperature-based counterparts.

Cropping and excavating dugongs target different seagrass species – leaves of temperate species and both the leaves and rhizomes of tropical species, respectively (Wirsing et al. 2007a) – so the divergent pattern of diving we observed could have been the product of changes in the quantity and/or quality of plants exploited by excavating individuals (Lanyon and Marsh 1995). We also consider this scenario to be unlikely. Optimal diving models predict positive correlation between patch quality and dive duration (Mori et al. 2002). Therefore, because the availability (biomass) of tropical leaves and rhizomes in Shark Bay peaks during the summer and then declines through the autumn and winter (Masini et al. 2001), we would have expected to observe longer dives by excavating dugongs during the height of the Austral summer if their diving behavior was driven by seagrass phenology. Instead, TAD for excavating individuals was at its lowest during summer months and increased through the autumn.

In conclusion, this field study helps to dispel the general notion, and the implicit assumption of the majority of optimal diving models, that diving behavior of large-bodied aquatic air-breathers is not influenced by predation risk. Therefore, studies that use diving behavior to infer spatiotemporal variation in characteristics of prey resources (e.g. habitat quality) or foraging effort may make incorrect conclusions if predation risk to divers varies in space and/or time. Furthermore, in conjunction with recent studies suggesting that adjustments by individual breath-hold divers under threat of predation are condition-dependent (Frid et al. 2006, 2009), our work highlights the complexity of anti-predator decision making by diving species by showing that responses of these species to danger can vary with foraging mode. Future studies that address the drivers of this complexity should improve the performance of optimal diving models. Such studies should also yield crucial insights about the consequences of declines in predator abundance for diver behavior and, because changes to patterns of resource exploitation by these species could cascade through communities (Boyd 1997, Heithaus et al. 2008), the dynamics of aquatic ecosystems. Without this insight, those responsible for the protection of exploited aquatic systems with depleted predator populations could underestimate the importance of predation and, therefore, fail to prevent further degradation or restore ecosystem integrity.

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