

## Can you dig it? Use of excavation, a risky foraging tactic, by dugongs is sensitive to predation danger

AARON J. WIRSING<sup>\*†‡</sup>, MICHAEL R. HEITHAUS<sup>‡</sup> & LAWRENCE M. DILL<sup>\*</sup>

<sup>\*</sup>Department of Biological Sciences, Behavioural Ecology Research Group, Simon Fraser University, Burnaby

<sup>†</sup>School of Animal Biology, University of Western Australia, Crawley

<sup>‡</sup>Department of Biological Sciences, Florida International University, North Miami

(Received 17 October 2006; initial acceptance 8 December 2006;

final acceptance 2 February 2007; published online 19 September 2007; MS. number: A10592R)

Foraging and vigilance are mutually exclusive for some foraging tactics but not others. Thus, in response to changes in predation danger, prey species with multiple foraging tactics may switch facultatively between them, allowing for differential levels of vigilance. Using data from focal observations collected over 4 years (2002–2004, 2006) in Shark Bay, Western Australia, we explored the use of two tactics, cropping and excavation, by dugongs, *Dugong dugon*, foraging under risk of predation by tiger sharks, *Galeocerdo cuvier*. Overall, dugongs predominantly used the cropping tactic, which allows for regular visual scans, to harvest temperate sea grass species. Dugongs only used the excavation tactic, which precludes regular visual scans but allows individuals to access the nutritious rhizomes of preferred tropical sea grass species, in months when tropical species were most available (February–May). However, during these months the time dugongs allocated to excavation was inversely related to shark abundance rather than the availability of these sea grass species. We conclude that use of foraging tactics by dugongs is sensitive to predation danger, and that individuals manage their risk of mortality via reduced use of a profitable but potentially hazardous tactic when the likelihood of encountering predators is high. Excavating dugongs are more likely to disrupt sea grass meadow structure and promote succession than are those engaged in cropping. Thus, by altering the time dugongs devote to these alternative tactics, tiger sharks may exert an indirect effect on sea grass patch composition and structure and, ultimately, benthic communities.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

**Keywords:** cropping; *Dugong dugon*; *Galeocerdo cuvier*; predation risk; vigilance

The act of foraging can limit the ability of prey animals to be vigilant (e.g. Krause & Godin 1996; Bednekoff & Lima 1998; Lima & Bednekoff 1999). Consequently, prey individuals under threat of predation often lose opportunities to acquire energy while scanning their environment (Lima & Bednekoff 1999). However, not all feeding modes constrain antipredator vigilance to the same degree (Bednekoff & Lima 1998; Kaby & Lind 2003). For example, foraging tactics that are complex (Kaby & Lind 2003) or that involve body postures restricting vision (Krause &

Godin 1996) are much more likely to impede predator detection and escape than those allowing simultaneous surveillance. It follows that prey animals may switch between foraging tactics in a threat-sensitive manner, avoiding tactics that preclude vigilance when danger is heightened (e.g. Helfman 1989). Predator-induced changes in the foraging tactics used by herbivores are of particular interest to ecologists, for they may alter the pressure that these species exert on plants and, ultimately, community structure (Crawley 1983; Schmitz et al. 2004). In marine systems, the influence of predation risk on the choice of foraging tactics by large herbivores has not been addressed.

Here, we explore the use of alternative foraging tactics by dugongs, *Dugong dugon*, under risk of predation by tiger sharks, *Galeocerdo cuvier*, in a Western Australian embayment (Shark Bay). Dugongs use two primary tactics to harvest sea grass: cropping, whereby clusters of leaves are stripped from the branching stems of sea grass plants

Correspondence and present address: A. J. Wirsing, Department of Biological Sciences, Marine Biology Program, Florida International University, Biscayne Bay Campus MSB 351, North Miami, FL 33181, U.S.A. (email: [wirsinga@fiu.edu](mailto:wirsinga@fiu.edu)). L. M. Dill is at the Department of Biological Sciences, Behavioural Ecology Research Group, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

(Anderson 1982), and excavation, whereby individuals root into the substrate with their rostra to consume both above- and below-ground (i.e. rhizomal) portions of sea grass plants (Anderson & Birtles 1978). In Shark Bay, dugongs crop the temperate sea grass species *Amphibolis antarctica* (Anderson 1986), which is widely available as food (~90% of total sea grass cover; Walker et al. 1988), while apparently using excavation foraging to consume tropical sea grass species (e.g. *Halodule uninervis*, *Halophila ovalis*) that are more sparsely distributed (Walker et al. 1988). Tropical sea grass species are generally preferred over temperate ones (i.e. dugongs feed on tropical sea grass patches to an extent greater than that predicted by their availability; Anderson 1986; Preen 1995), probably because their rhizomes are energy rich and contain relatively high concentrations of important nutrients (e.g. organic carbon; de longh et al. 1995). Thus, dugongs engaged in excavation may achieve higher energy intake rates than those using the cropping tactic. However, while the act of cropping allows for frequent scans between bites A. Wirsing (personal observation), the process of excavation involves lengthy periods of digging that undoubtedly preclude vigilance. Moreover, excavating dugongs usually produce large sediment plumes that are likely to impede surveillance and could attract predators. Consequently, dugongs electing to excavate in areas where, and during time periods when, both tactics are feasible may pay the cost of increased mortality risk (see Godin & Smith 1988 for an example of such a cost in foraging guppies, *Poecilia reticulata*). The magnitude of this cost is not constant, however, as tiger shark abundance in Shark Bay shows strong seasonal variation (Heithaus 2001; Wirsing et al. 2006).

We tested the hypothesis that dugongs manage their risk of mortality by using the dangerous but profitable foraging tactic (excavation) in inverse proportion to the likelihood of encountering predators. The biomass of tropical sea grass species in Shark Bay is linked to water temperature, being greatest at the peak of the warm season (January–February) and declining sharply during months when water temperatures are below 20°C (June–October; Anderson 1986; Walker & McComb 1988). Consequently, dugongs generally do not excavate tropical species during these cold months, cropping *A. antarctica* instead (Anderson 1986). Accordingly, our hypothesis predicts that when excavation is feasible (i.e. November–May), the time dugongs allocate to excavation while foraging should be inversely related to tiger shark abundance. Conversely, if the time dugongs devote to excavation is driven solely by the availability of tropical sea grass species, then we would expect the frequency with which this tactic is used to be greatest during months when water temperatures are highest (i.e. January–March). Given that tiger shark abundance and temperature are positively correlated (Heithaus 2001), an inverse relationship between shark abundance and excavation time during these months should not exist under this latter scenario (i.e. time allocated to excavation should be maximal when both shark abundance and temperature are highest). In addition to looking at foraging tactics, we also asked whether the overall time that dugongs spent foraging corresponded with changes in shark abundance and/or water temperature.

## METHODS

### Study Site

This study was conducted in the Eastern Gulf of Shark Bay, offshore of the Monkey Mia Dolphin Resort (~25°45'S, 113°44'E). Shark Bay has been listed as a World Heritage Area since 1991, and is home to a large dugong population (between 10 000 and 14 000 individuals; Marsh et al. 1994; Preen et al. 1997; Gales et al. 2004), many of which use our study area (abundance varies from a few dozen in winter to a few hundred in summer; Wirsing et al., in press). Thus, we were able to evaluate the foraging decisions of dugongs belonging to a healthy population under relatively pristine conditions.

### Dugong Foraging Behaviour

Over the course of 4 years (2002–2004, 2006), we assessed the foraging behaviour of individual dugongs using focal animal follows ( $N = 167$ ; Altmann 1974). Individual adults sighted randomly during transect passes through shallow and deep habitat (see Wirsing et al., in press, for methodological detail) were targeted for focal observation, minimizing the likelihood that starting positions were spatially biased (Heithaus et al. 2006), and focal follows were only conducted in Beaufort wind conditions  $\leq 1$  to facilitate reliable observation. Dugongs selected for behavioural observation were approached at slow speed (~1 km/h) and then allowed to acclimate to our vessel (a 4.5-m runabout) for 5 min from a distance of roughly 50 m; subsequently, behavioural observations were made from a distance of 10–20 m. We are confident that this method of observation was minimally invasive: focal animals rarely changed their behaviour or moved in response to our approach, they moved freely about the vessel without investigating, and often rested in close proximity to the boat, implying that we were perceived neither as a distraction nor as a threat. Dugongs that did respond to our approach by moving off or changing their behaviour (i.e. by terminating foraging or resting bouts;  $N = 5$ ) were not followed. Focal observation periods lasted an average  $\pm$  SD of  $52.2 \pm 21.6$  min; follows that lasted less than 30 min ( $N = 23$ ) were not included in this analysis, resulting in 144 usable follows. During each follow, we recorded water depth (m) and the position (with a GPS) and predominant behaviour (foraging, travelling, resting, unknown) of the focal individual every 2 min. When animals could not be observed while submerged, activity states were distinguished using diagnostic behaviour and characteristics at the surface (Anderson 1986; Chilvers et al. 2004). Foraging individuals typically engaged in slow, meandering searches with irregular surface intervals and often were associated with sediment plumes and deep dives, while resting individuals showed little displacement, regular surface intervals, and shallow and relaxed breaths. Travelling individuals generally showed directional movement with few/no stops and regular surface intervals. In shallow habitat ( $\leq 4.5$  m in depth), we also noted whether foraging animals cropped or excavated sea grass during each 2-min observation interval. These two tactics proved easy to

distinguish when used in the shallows: dugongs that engaged in cropping tended to meander and take haphazard bites of sea grass, while excavating animals tended to confine their foraging effort to particular areas and usually created large sediment plumes (note that cropping was never assumed simply because of the absence of a plume). When possible, unique marking and scarring patterns (Anderson 1995) were recorded during each follow to ensure that individuals were not sampled repeatedly.

Data collected using focal follows are often autocorrelated, as all behavioural observations are constrained by the behaviour of the focal animal when the follow is initiated unless observations are separated by long intervals (Manly et al. 1993). We believe that our assessment of dugong foraging behaviour is robust to this potential problem, however, given that (1) follows were initiated randomly with respect to location and behavioural state, and (2) the focal data we collected were subject to a consistent level of bias (i.e. there was no reason to assume that levels of autocorrelation characterizing our follow data changed over time), allowing reliable comparison of foraging budgets associated with varying levels of predation danger and water temperature.

## Predator Abundance

Catch rates provide an index of tiger shark abundance in Shark Bay (Heithaus 2001; Wirsing et al. 2006). Sharks were caught on 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 ( $\sim 160 \text{ km}^2$ ); all sharks caught throughout the day were measured (total length, TL), tagged and released (for methodological detail, see Heithaus 2001; Wirsing et al. 2006). Because of notable ontogenetic shifts in tiger shark diets (e.g. Lowe et al. 1996), tiger sharks under 3.0 m total length (TL) are not likely to pose a threat to dugongs. Thus, only sharks  $> 3.0 \text{ m}$  TL were used to calculate daily catch rates. Note, however, that the inclusion of sharks falling below this size threshold does not change the results presented below.

Our fishing effort was intensive and consistent (Wirsing et al. 2006). However, the frequency with which sharks were fished ( $\sim 6$  fishing days/month) precluded a continuous (daily) evaluation of the relationship between the foraging budgets of focal individuals and predator numbers. Thus, in light of the strong seasonal pattern in shark abundance in our study area (Heithaus 2001), we used a sinusoidal function with a period of 1 year to predict the annual trend in daily catch rates (sharks/h). Catch data used in the model were combined for the years 2002–2004 and 2006 because interannual variation was not detected after accounting for seasonal effects (ANCOVA:  $F_{2,117} = 0.97$ ,  $P = 0.38$ ). The model was fitted 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. Each focal follow was assigned a shark catch rate (i.e. a predation risk level) generated by the model, which has been shown to have explanatory value in this system (Wirsing et al. 2007).

## Statistical Analysis

The dependent variables in this study were expressed as (1) the number of 2-min observation intervals during which focal animals engaged in foraging, divided by the total number of observation intervals for the follow, and (2) the number of intervals during which animals engaged in excavation foraging, divided by the total number of intervals during which foraging occurred in the shallows. For the latter dependent variable, follows during which the focal individual engaged in shallow-water foraging for fewer than five observation intervals were deleted from the data to avoid bias stemming from low sampling time. For both variables, data from the 4 years of the investigation were analysed collectively because annual differences between times devoted to foraging (ANOVA:  $F_{3,140} = 0.35$ ,  $P = 0.79$ ) and excavation ( $F_{3,59} = 2.38$ ,  $P = 0.08$ ) were not detected.

We examined the extent to which models based solely on predator (tiger shark) abundance, solely on sea surface temperature ( $^{\circ}\text{C}$ ; measured daily from a constant location within the study area), and on the combination of these two factors could predict each of the dependent variables using information theoretical methodology (Burnham & Anderson 1998; Anderson et al. 2000). This approach ranks models of the relationship between dependent and explanatory variables according to fit, while accounting for differences in complexity, and therefore allows for rigorous comparisons of competing hypotheses (Anderson et al. 2000; Johnson & Omland 2004). Linear models of the two dependent variables were fit using maximum likelihood; since both dependent variables were proportions with a modal value of zero, a low mean and large variance, a binomial error distribution served as the basis for statistical inference (Lloyd 1999). Although correlated, the two independent variables were sufficiently divergent to allow for independent assessment in the models. The support for each model was quantified using Akaike's Information Criterion, corrected for small sample size ( $\text{AIC}_c$ ; Burnham & Anderson 1998; Anderson et al. 2000); nonlinear transformations of the independent variables were applied post hoc if they substantially improved the support for a given model (i.e. lowered its  $\text{AIC}_c$  by  $\geq 2$ ; Burnham & Anderson 1998). Akaike weights ( $w$ ), which measure the probability that a particular model is best among a set of competitors, and the change in  $\text{AIC}_c$  between models ( $\Delta\text{AIC}_c$ ), were used to assess model uncertainty (Burnham & Anderson 1998).  $R^2$  analogues for models analysed using maximum likelihood ( $R_L^2$ ; calculated as one minus the percentage difference in the negative log-likelihood value for the model in question and the constant-only model) were used to index the amount of variation in the dependent variable explained by each model. Finally, when presented, coefficient estimates for model parameters are accompanied by 95% confidence intervals (SYSTAT 10, SPSS Inc., Chicago, IL, U.S.A.).

## RESULTS

### Foraging

The 144 individual dugongs that were subject to focal observation ( $\geq 30 \text{ min}$ ) devoted an average  $\pm \text{SD}$  of  $49.74$

$\pm 35.97\%$  (min = 0, max = 100%) of their time to foraging. The best model of time allocated to foraging by dugongs included only sea surface temperature ( $T$ ; Table 1). However, this model was not clearly superior to its competitors (Table 1), preventing a firm conclusion that temperature exerted a stronger influence on dugong foraging time than did tiger shark abundance. Moreover, none of the competing models could explain more than 0.20% of the observed variation in the time that individual dugongs devoted to foraging (Table 1), implying that correspondence between trends in temperature and large tiger shark abundance and the pattern of foraging we observed was relatively weak (i.e. individual foraging times were governed primarily by factors not included in the model). Indeed, while water temperature and shark abundance varied dramatically over the course of the investigation (Wirsing et al. 2006), the time that dugongs budgeted to foraging remained fairly consistent (Fig. 1).

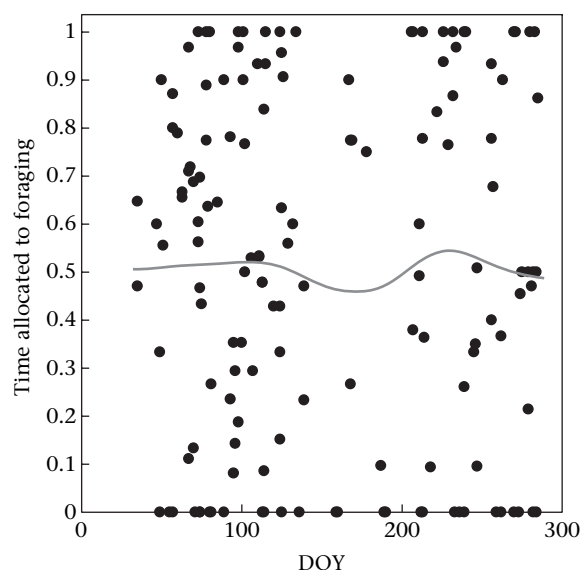
## Excavation

Excavation was not observed in any year during months when temperatures typically fell below 20°C (June–October). Thus, our analysis of the time that dugongs devoted to this tactic necessarily excluded these months. During months when excavation did occur (February–May of all years), a total of 63 dugongs foraged in shallow habitat (<4.5 m in depth) for a minimum of five observation intervals while being followed. These individuals allocated an average  $\pm$  SD of  $20.93 \pm 34.79\%$  (min = 0, max = 100%) of their shallow habitat foraging time to excavation. The time that dugongs devoted to excavation was predicted equally well by a model that included both sea surface temperature and large tiger shark abundance ( $S + T$ ) and a model that included shark abundance alone ( $S$ ) (Table 2). Each model explained a considerable amount of the variation in excavation time (26% and 25%, respectively), and both were clearly superior to the other models under

**Table 1.** Models of the time devoted to foraging by dugongs in Shark Bay, Western Australia over a period of 4 years

Model	$K$	$\Delta$	$w$	$R_L^2$
<b>T</b>	<b>1</b>	—	<b>0.512</b>	<b>0.002</b>
S+T	2	1.275	0.271	0.002
S	1	3.020	0.113	0.001
Constant-only	0	3.165	0.104	—

Foraging data were collected using focal animal follows ( $N = 144$ ) exceeding 30 min. Models were generated using all linear combinations of two independent variables: large (>3 m total length) tiger shark abundance ( $S$ ) and sea surface temperature ( $T$ , °C). The dependent variable, the proportion of 2-min observation intervals during which foraging was the dominant behaviour, featured a constrained maximum and a modal value of zero. Thus, models were fit with binomial regression, and then ranked using Akaike's Information Criterion, corrected for small sample size ( $AIC_c$ ). For each model,  $K$  is the number of fitted parameters in the model,  $\Delta$  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 probability of preeminence), and  $R_L^2$  is the  $R^2$  analogue for models analysed using maximum likelihood.



**Figure 1.** Relationship between the proportion of time allocated to foraging by dugongs during focal animal follows ( $N = 144$ , ●) and day of year (DOY) over a period of 4 years (2002–2004, 2006; note that the months of November–January were not analysed). The grey trend line was generated using distance-weighted least squares smoothing (DWLS, tension 1.0, SYSTAT 10).

consideration (Table 2). The large gap in efficacy between the model based solely on shark numbers and that based solely on temperature indicates that predator abundance was a reliable predictor of the use of excavation by dugongs during the months of February–May, and that the inclusion of temperature information within this time interval did not improve the predictive capacity of the shark-based model. The fit of both models was improved substantially using post hoc nonlinear (quadratic) transformations ( $\Delta AIC_c$  values > 2). Following transformation, the coefficient estimates for the shark abundance variable in both models were positive (full model:  $113.47 \pm 83.93$ ; shark-only model:  $124.76 \pm 76.15$ ), while the coefficients for the quadratic terms were negative (full model:  $-4023.53 \pm 2181.53$ ; shark-only model:  $-4722.25 \pm 1819.46$ ). By implication, during months when excavation was observed,

**Table 2.** Models of the time devoted (i.e. proportion of 2-min observation intervals allocated) to excavation by dugongs foraging in shallow sea grass habitat (<4.5 m in depth) between February and May over 4 years

Model	$K$	$\Delta$	$w$	$R_L^2$
<b>S + T</b>	<b>4</b>	<b>0.000</b>	<b>0.543</b>	<b>0.257</b>
S	2	0.348	0.457	0.252
T	2	51.134	0.000	0.196
Constant-only	0	222.870	0.000	—

Foraging data were collected using focal animal follows exceeding 30 min ( $N = 63$ ). Models were generated using all combinations of tiger shark abundance ( $S$ ) and sea surface temperature ( $T$ , °C), fit with binomial regression, and then ranked using Akaike's Information Criterion, corrected for small sample size ( $AIC_c$ ); nonlinear (quadratic) transformation applied post hoc substantially improved the fit of all models (i.e.  $\Delta AIC_c$  values > 2). See Table 1 caption for symbol definitions.



dugongs reduced their reliance on this tactic as shark abundance rose (Fig. 2). Importantly, the coefficient estimates for the temperature variable ( $-1.04 \pm 2.55$ ) and its quadratic term ( $0.02 \pm 0.055$ ) in the full model were not distinguishable from zero, indicating a lack of temperature effect.

## DISCUSSION

The results of this investigation are consistent with the hypothesis that use of particular foraging tactics by dugongs is sensitive to the danger of predation. Overall levels of foraging by dugongs were temporally consistent. However, during warm months (February–May) when the sea grass species typically excavated by dugongs in Shark Bay (i.e. tropical species, *Halodule uninervis*, *Halophila ovalis*; Anderson 1986) were most available, individuals significantly reduced their use of this tactic (and devoted more time to cropping) when large tiger sharks were most abundant, presumably because the process of excavation inhibits vigilance and may even attract predators. Thus, we conclude that dugongs manage their risk of death by avoiding a profitable but risky feeding tactic when the likelihood of predator encounter is elevated.

The excavation times we observed were characterized by marked heterogeneity (Fig. 2). Moreover, our analysis did not address other factors that are likely to influence its use (e.g. condition dependence, fine-scale patterns of resource distribution and abundance). Thus, the fact that shark abundance alone explained roughly a quarter of the observed variation in the use of this tactic between

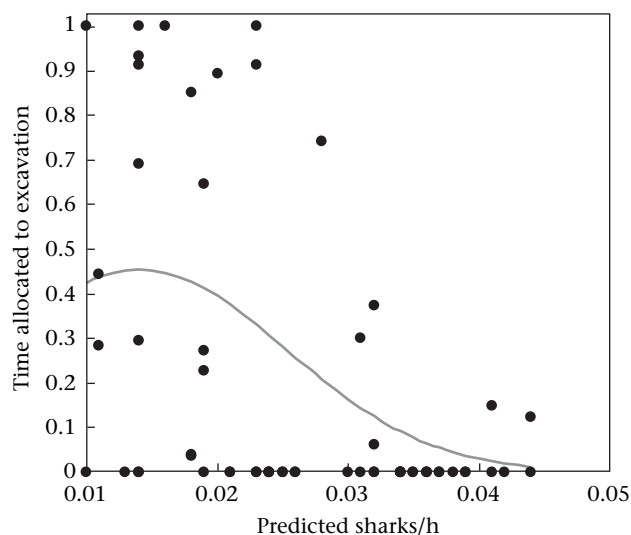
February and May is remarkable and underscores the strength of the relationship between the willingness of dugongs to excavate sea grass and their perceived risk from tiger sharks.

Previous work has shown that tropical sea grass species are sparsely distributed, of low biomass, and generally unavailable during months when water temperatures are below 20°C in our study area (Walker & McComb 1988; Walker et al. 1988). In accord with our assumption that dugongs use excavation to target these rare but nutritious species, we found that foragers tended to use this tactic in sea grass patches where the presence of these species has been documented (Walker et al. 1988), they generally devoted little time to excavation while harvesting sea grass, and ceased using this tactic between June and October. The comparatively heavy use of excavation by dugongs during the latter stages of the warm season (i.e. mid-April–May, predicted shark catch values between 0.01 and 0.02 sharks/h; Fig. 2), when tropical sea grass species are still available and tiger shark abundance has dropped to intermediate levels (Wirsing et al. 2006), suggests that foragers would probably spend more time harvesting the energy-rich rhizomes of these species throughout the warm season, despite their relative scarcity, were it not for the influence of risk from tiger sharks.

We were unable to determine whether dugongs under focal observation excavated sea grass while foraging in deep habitat. This methodological shortcoming could have biased the results presented herein if episodes of deep water excavation were missed frequently. We are confident, however, that use of this tactic was largely restricted to the shallows because (1) the tropical sea grass species putatively targeted by dugongs using this tactic are found primarily in shallow habitat (Anderson 1986; Walker et al. 1988), (2) sediment plumes that often accompany excavation were never witnessed during observations of individuals feeding in deep water (even when water clarity was excellent and conditions were calm), and (3) deep-habitat foraging was relatively infrequent (i.e. <10% of total foraging time; A. Wirsing, unpublished data) during periods when excavation was used most often in the shallows (mid-April–May).

Despite marked variation in the abundance of their major local predator, on average, dugongs budgeted approximately half of their time to foraging over the course of this investigation. This result, which is consistent with the findings of several previous dugong tracking studies (e.g. Churchward 2001; Chilvers et al. 2004), may mean that these sirenians do not sacrifice diurnal feeding time to be more vigilant during periods of high mortality risk. Dugongs may be unable to dramatically alter their feeding schedule given the generally poor quality of their diet (Best 1981; Marsh et al. 1984) and the fact that their relatively slow rate of digestion probably limits the amount of sea grass that can be ingested (Lanyon & Marsh 1995).

Predators often select unwary prey (Krause & Godin 1996). For prey animals that have been targeted, even slight delays in escape can mean the difference between life and death (Kaby & Lind 2003). Thus, in general, we would expect prey individuals to reduce their use of



**Figure 2.** Relationship between the proportion of time allocated to excavation foraging in shallow habitat (<4.5 m in depth) by dugongs during focal follows ( $N = 63$ , ●) and large tiger shark (>3 m) catch rate (sharks/h). Note that the range of shark catch rates presented coincides with the time span over which excavation was observed (February–May of all years). The grey trend line represents a prediction furnished by the quadratic model  $Y$  (time allocated to excavation) =  $\exp -1.59 + 124.76 \times (\text{shark abundance}) - 4722.25 \times (\text{shark abundance}^2)$ .

foraging tactics that, by virtue of their complexity or the body position they require, prevent antipredator vigilance when the likelihood of predatory attack is high. Conversely, when their environment is safe, prey should allocate their time to such foraging modes in a manner that is independent of spatial and temporal variation in predation risk (Nolet et al. 2006). Dugongs seem to conform to this expectation: individual foragers relied less on excavation, a tactic that enables dugongs to access the nutritious rhizomal portions of tropical sea grass species but precludes frequent scans of the environment, when large tiger sharks were abundant. This predator-mediated shift in the use of alternative foraging tactics by dugongs is noteworthy for several reasons. (1) It adds dugongs to the growing list of species that eschew dangerous foraging tactics when there is need for defensive investment for other examples, see (Kotler et al. 2002; Olsson et al. 2002), even though previous enquiries have ignored predation risk and discussed the feeding modes of this sirenian solely in relation to the availability of various sea grass species (e.g. Anderson & Birtles 1978; Anderson 1982, 1986; Preen 1995). (2) It suggests that the foraging behaviour of other marine species widely believed to be relatively immune to predation may, nevertheless, be sensitive to predation risk. (3) It has important implications for the relationship between dugongs and the sea grass meadows upon which they subsist. Excavation feeding by dugongs can radically disrupt the structure of sea grass meadows, leaving deep furrows and denuded patches that promote succession (de Jongh et al. 1995; Preen 1995; Nakaoka & Aioi 1999; Masini et al. 2001). In contrast, dugongs engaged in cropping are believed to be less disruptive, because they only remove the terminal portions of sea grass plants, leaving the rhizomes intact and likely promoting the persistence of perennial sea grass species (Anderson 1986). Thus, by influencing the time that dugongs allocate to these two tactics, tiger sharks may exert a strong indirect influence on the dugong's food (i.e. the sea grass beds themselves). During periods when an abundance of sharks forces dugongs to allocate relatively high amounts of time to cropping, for example, the extent to which dugong feeding facilitates the intrusion of pioneering sea grass species may decline markedly. We can surmise, then, that alterations in the dynamics of tiger shark populations where this predator coexists with dugongs are likely to have a profound effect on the composition of local sea grass meadows and, ultimately, benthic community structure and function.

### Acknowledgments

We thank R. Abernethy, V. Alla, T. Bujas, C. Chow, M. Davis, A. Greenley, K. Harper, L. Heithaus, M. Kerford, S. Kowalewsky, A. Krickan, J. Lasky, L. Marshall, K. Martin, R. McPhie, B. Stalvey, J. Wilder and K. Wirsing for field assistance. This material is based on work supported by the National Science Foundation under Grant no. 0526065. Other grants and support were provided by Humminbird, Mercury Marine Australia, the Monkey Mia Dolphin Resort, Monkey Mia Wildsights (Shotover), the National Geographic Society Expeditions Council, National

Geographic Remote Imaging, the National Science Foundation (OCE-526065), Natural Sciences and Engineering Research Council of Canada (NSERC grant A6869 to L.M.D.), PADI Foundation, Shakespeare Electronics, the Shark Bay Fish Factory, the University of Western Australia, and public donations. We are grateful to I. Anderson, C. Beck, K. Crane, A. Fraser, I. Gordon, D. Rose and D. Witt for logistical support, D. Charles for support and advice, D. Capewell and the Yadgalah Aboriginal Corporation for information about dugongs, D. Massey for extra field accommodations, H. Raven for temperature data, D. Blumstein, J. Brown, E. Elle, B. Sargeant and an anonymous referee for helpful reviews, B. Smith and T. Steury for statistical help, B. Black for his generosity and hospitality, and the denizens of the Dill lab for helpful suggestions. This research was conducted under the authority of Fisheries Western Australia permit 08/01, Western Australia Department of Conservation and Land Management permits SF003818, SF004228, SF004542, SW008085, and renewals, and Florida International University and Simon Fraser University Animal Care permits. This paper is contribution no. 28 of the Shark Bay Ecosystem Research Project.

### References

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–267.
- 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 sub-surface observations. *Australian Wildlife Research*, **9**, 85–100.
- 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.
- Anderson, P. K. & Birtles, A. 1978. Behavior and ecology of the dugong, *Dugong dugon* (Sirenia): observations in Shoalwater and Cleveland Bays, Queensland. *Australian Wildlife Research*, **5**, 1–23.
- Bednekoff, P. A. & Lima, S. L. 1998. Randomness, chaos, and confusion in the study of antipredator vigilance. *Trends in Ecology & Evolution*, **13**, 284–287.
- Best, R. C. 1981. Food and feeding habits of wild and captive Sirenia. *Mammal Review*, **11**, 3–29.
- 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.
- Churchward, C. 2001. The effects of depth and activity type on dugong (*Dugong dugon*) diving behaviour in Shark Bay, Western Australia. M.S. thesis, The University of Calgary.
- Crawley, M. J. 1983. *Herbivory*. Los Angeles, California: University of California Press.
- 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.

- Godin, J. G. J. & Smith, S. A. 1988. A fitness cost of foraging in the guppy. *Nature*, **333**, 69–71.
- Heithaus, M. R. 2001. 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., 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.
- Helfman, G. S. 1989. Threat-sensitive predator avoidance in damselfish—trumpetfish interactions. *Behavioral Ecology and Sociobiology*, **24**, 47–58.
- de Jongh, 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 & Evolution*, **19**, 101–108.
- Kaby, U. & Lind, J. 2003. What limits predator detection in blue tits (*Parus caeruleus*): posture, task, or orientation? *Behavioral Ecology and Sociobiology*, **54**, 534–538.
- Kotler, B. P., Brown, J. S., Dall, S. R. X., Greser, S., Ganey, D. & Bouskila, A. 2002. Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. *Evolutionary Ecology Research*, **4**, 495–518.
- Krause, J. & Godin, J. G. J. 1996. Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey. *Behavioral Ecology*, **7**, 264–271.
- Lanyon, J. M. & Marsh, H. 1995. Digesta passage times in the dugong. *Australian Journal of Zoology*, **43**, 119–127.
- Lima, S. L. & Bednekoff, P. A. 1999. Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? *Animal Behaviour*, **58**, 537–543.
- Lloyd, C. J. 1999. *Statistical Analysis of Categorical Data*. New York: Wiley.
- 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.
- Manly, B. F. G., McDonald, L. L. & Thomas, D. L. 1993. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. London: Chapman & Hall.
- 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.
- 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.
- 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.
- Nolet, B. A., Fuld, V. N. & van Rijswijk, M. E. C. 2006. Foraging costs and accessibility as determinants of giving-up densities in a swan-pondweed system. *Oikos*, **112**, 353–362.
- Olsson, O., Brown, J. S. & Smith, H. G. 2002. Long- and short-term state-dependent foraging under predation risk: an indication of habitat quality. *Animal Behaviour*, **63**, 981–989.
- 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.
- 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.
- 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. 2007. Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. *Animal Behaviour*, **74**, 93–101.
- Wirsing, A. J., Heithaus, M. R. & Dill, L. M. In press. Fear factor: dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*). *Oecologia*. doi:10.1007/s00442-007-0802-3.