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

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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.

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

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(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 Iongh 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 ≤ 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 ± SD of 52.2 ± 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