Review Article

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Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals

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ABSTRACT

The notion that predators can affect their prey without killing them is widely supported in the ecological literature yet rarely applied by marine mammal studies. We present three case studies in which patterns of time allocation by individual marine mammal foragers were used to index the sublethal effects of predators on bottlenose dolphins (*Tursiops* sp.), harbor seals (*Phoca vitulina*), and dugongs (*Dugong dugon*). In each case, foraging individuals optimized energy gain and safety from predators by spending less time in more profitable but dangerous patches or decreasing their use of risky feeding tactics that would increase net energy gain. By implication, marine mammals are subject to the non consumptive effects of their predators (*i.e.*, to intimidation), and fear can mediate their impacts on their resources. We suggest, therefore, that future studies quantify patterns of time allocation to measure sublethal effects of predators on marine mammals, as well as the capacity of

marine mammals to have sublethal effects on their own prey. We argue that such an approach is important because non consumptive effects may be of greater magnitude than lethal effects of predators, and information on sublethal effects of predators can inform conservation plans and studies of community structure.

Key words: bottlenose dolphin, *Tursiops*, dugong, *Dugong dugon*, harbor seals, *Phoca vitulina*, intimidation, predation risk, time allocation, trait-mediated indirect interactions.

Predators affect prey populations most obviously by killing and consuming individuals. Thus, studies of the ecological role of upper trophic level predators in natural communities have focused primarily on the indirect effects they exert on resources when removing intermediate consumers (Abrams 1995, Luttbeg and Kerby 2005). An alternative, but not mutually exclusive, paradigm suggests that predators also affect prey populations non consumptively by intimidating their potential targets (Brown *et al*. 1999) and that alterations in resource abundance stemming from defensive adjustments by frightened consumers can lead to changes in community composition and dynamics rivaling or exceeding those resulting from predator-induced reductions in prey density (Peacor and Werner 2001, Werner and Peacor 2003, Schmitz *et al*. 2004, Preisser *et al*. 2005). By implication, studies that focus on patterns of prey consumption and ignore the effects of fear may underestimate the overall impact predators have on their communities (Peacor and Werner 2001, Dill *et al*. 2003).

Examples of predator intimidation and its importance in structuring terrestrial and aquatic communities abound (Werner and Peacor 2003, Schmitz *et al*. 2004, Preisser *et al*. 2005, Verdolin 2006) but remain poorly documented in marine systems, especially among vertebrates (Dill *et al*. 2003). Of particular note is the scant attention given to intimidation by marine mammals as upper trophic level predators and the possibility that they are fearful of predators themselves. Such interactions are important because these strongly interactive species (*sensu* Soulé *et al*. 2003) may alter community dynamics by initiating trait modification in their prey and by transmitting the indirect effects of their predators to lower trophic levels when they shift their foraging and space use patterns in response to danger. Indeed, even recent studies addressing possible ecosystem effects of marine mammals often have not considered their potential either to scare prey (*e.g.*, Jackson *et al*. 2001, Springer *et al*. 2003, Morissette *et al*. 2006, Zerbini *et al*. 2006) or to be scared by predators (*e.g.*, Preen 1995, Estes *et al*. 2004). This trend probably stems, in large part, from the rarity with which interactions between marine mammals and their predators are observed and the lack of widely accepted and applicable methods for addressing the role of fear in the lives of marine mammals and their prey (Bowen 1997). Accordingly, we (1) advocate the measurement of time allocation by foraging prey, an approach that has yielded tremendous insight regarding the ecology of terrestrial mammals, and (2) illustrate its utility in marine environments with examples from our work in two systems—Shark Bay, Western Australia, and Prince William Sound, Alaska.

Tools for Quantifying the Fear Generated and Experienced by Marine Mammals

In the absence of observed mortality, how do we establish that predators affect their prey and, ultimately, communities? To date, outside of the lab, ecologists have

addressed this question primarily through the use of mesocosm experiments, where simple communities (*e.g.*, predator + prey + prey resource) are constructed, predator lethality (*i.e.*, the degree to which they can consume, rather than simply scare, prey) is manipulated, and prey and resource responses under various scenarios are then compared (see Werner and Peacor 2003 for a review). These experiments, which provide evidence of predator intimidation if trophic cascades manifest themselves even when consumption of prey individuals by predators is minimal or non existent, work well with small-bodied species and in confined systems. However, they are difficult to perform in large scale, open systems involving large, highly mobile predator and prey species where experimental manipulation is impossible and confounding factors cannot easily be controlled—precisely the situation for most marine mammals. Fortunately, within the framework of optimality theory, the non consumptive effects of predators also can be indexed in the field using both the time allocated to foraging patches and the time devoted to apprehensive behavior within a patch by consumers (Brown 1999).

While acquiring resources, a forager may succumb to predation. Thus, the benefits accrued by a forager using a patch must be weighed against its likelihood of being killed by a predator during the foraging bout (*i.e.*, predation is a foraging cost; Brown *et al*. 1999, Brown and Kotler 2004). For consumers that are either invulnerable or occupy environments were resource abundance and predation risk are not positively correlated, the foraging cost of predation is negligible, so we expect them to forage in a manner that maximizes energy or nutrient gain (Fraser and Gilliam 1987, Nonacs and Dill 1990). However, levels of resource availability and predation risk usually do covary positively (Brown and Kotler 2004). Consequently, foragers typically must seek to balance the conflicting demands of nourishment and predator avoidance optimally by trading food for safety (Sih 1980, Lima and Dill 1990, Lima 1998). Individual foragers can do so by allocating less time to dangerous feeding patches, *vs*. safer but relatively impoverished ones, and by allocating more time to apprehensive behavior (*e.g.*, vigilance) while using dangerous but energy-rich patches (Brown 1999). In the former case, the difference between the foraging time allocated to a particular patch and that expected based on food supply (or quality) alone serves as a proxy for the strength of intimidation (*i.e.*, the more fear a forager experiences in a patch, the more food it will exchange for increased safety elsewhere; "hazardous duty pay," Brown and Kotler 2004), while equivalence between observed and expected values supports the null hypothesis that consumers are not affected by fear (Abrahams and Dill 1989, van Baalen and Sabelis 1993). In the latter case, the magnitude of intimidation in a patch can be indexed using the difference between observed and baseline levels of apprehension (Laundré *et al*. 2001). Both of these behavioral metrics have been used successfully to address the role of fear in terrestrial mammals in the field.

For example, Brown *et al*. (1994) used differences in patch allocation times to evaluate the influence of predator intimidation on foraging microhabitat selection by granivorous rodents (Merriam's kangaroo rats, *Dipodomys merriami*; round-tailed ground squirrels, *Spermophilus tereticaudus*; greater Egyptian sand gerbils, *Gerbillus pyramidum*; Allenby's gerbils, *G. allenbyi*) in the Negev and Sonoran deserts. In both deserts, individual rodents can elect to harvest seeds in one of two major feeding microhabitats: bush microhabitats, where exposure to snake predators is elevated (Kotler *et al*. 1993), and open microhabitats, where exposure to avian predators is relatively high (Kotler *et al*. 1991). Feeders with equivalent seed densities were

placed in each microhabitat, allowing the authors to quantify the amount of food remaining following visitation by a rodent (*i.e.*, giving-up densities, GUDs; Brown 1988). Because consumers deplete patch resources over time, GUDs provide a measure of the time devoted to particular patches by foragers (*e.g.*, a high GUD signifies a relatively brief foraging bout and *vice versa*; Kotler *et al*. 2004). Consequently, if initial food densities are equal, observed disparities between patch-specific GUDs approximate the degree to which relative use of alternative patch types is driven by non-food factors, including predator intimidation (Brown 1988). Moreover, for any one patch, the degree to which an observed GUD exceeds that predicted by energetic requirements alone can provide a measure of the amount of time sacrificed by a visiting forager in return for enhanced safety elsewhere (Brown *et al*. 1994). Overall, Brown *et al*. (1994) found that, after controlling for food supply, significantly more time typically was allocated to foraging in bush than in open microhabitats, and that observed foraging times in both microhabitats generally were far lower than those expected based on energetic requirements alone (*i.e.*, that substantial amounts of food were being abandoned in both microhabitats). Hence, the authors concluded that (1) fear of avian predation generally is stronger than fear of snake predation among the rodents tested, leading to overuse of bush feeding microhabitats by individual foragers, and (2) use of both foraging microhabitats by rodents is influenced heavily by predation risk, meaning that fear of predation likely exerts a strong effect on spatial patterns of granivory and, ultimately, the structure of both of the communities under investigation.

Using levels of apprehension in particular foraging patches, Laundré *et al*. (2001) asked whether predation risk from reintroduced wolves (*Canis lupus*) influenced the behavior of two potential prey species (elk, *Cervus elaphus*; bison, *Bison bison*) in Yellowstone National Park, U.S.A. Relative to baseline levels characterizing the period when wolves were absent from the park, female elk and bison significantly elevated the time they allocated to apprehension (vigilance) while using foraging patches known to be frequented by their predators. Given that resource acquisition and antipredator vigilance often are mutually exclusive activities (Bednekoff and Lima 1998, Brown 1999), the authors concluded that increased fear of predation following the repatriation of wolves likely has altered the foraging efficiency of two of Yellowstone National Park's large herbivores and, as a result, initiated widespread changes in plant community composition (Ripple and Beschta 2005).

For any given area or time period, predation risk is a product of predator encounter rates and intrinsic habitat risk (*i.e.*, the conditional probability of prey death following an encounter) (Brown and Kotler 2004). Thus, in some counter intuitive cases, areas with high predator densities may actually be perceived as safe by prey individuals if they also afford high levels of protective cover or facilitate escape (*e.g.*, Heithaus and Dill 2006, Wirsing *et al*. 2007*a*). Similarly, time periods perceived to be dangerous may elicit high levels of anti-predator vigilance, low levels of predator attack success and, as a result, feature relatively few prey deaths. Accordingly, we caution that measures failing to incorporate all of the components of risk (*e.g.*, predator density, predator attack rates, prey death rates) should not be used in lieu of consumer behavior to quantify the effects of fear.

Marine Mammal Case Studies

Over the past several years, we have used patterns of time allocation to assess the non consumptive effects of predators on a variety of prey species in two marine

systems: Shark Bay, Western Australia, and Prince William Sound, Alaska. Here, we present three examples of our work, each involving a marine mammal, which we believe demonstrate (1) the utility of our approach, particularly where observations of predator–prey interactions are impractical, (2) that fear affects the lives of large marine vertebrates experiencing low levels of predator-induced mortality, and (3) that the results of studies addressing the effects of predator intimidation can help elucidate the forces structuring marine communities.

*Case study 1:—Habitat use by bottlenose dolphins (*Tursiops aduncus*) in Shark Bay*—Our 160 km^2 study area in the Eastern Gulf of Shark Bay (~25°45′S, 113°44′E) is used by approximately 300 bottlenose dolphins (Heithaus and Dill 2002). These cetaceans forage in two major habitats: deep channels (>6 m in depth) and shallow banks (<4 m in depth). Fish biomass is consistently greatest in shallow habitat, but so, too, is the abundance of the dolphin's only local predator, the tiger shark (*Galeocerdo cuvier*) (Heithaus and Dill 2002, Heithaus *et al*. 2002). Use of the study area by tiger sharks tends to be heavy during the Austral warm season (September–May) and relatively light during most, but not all, cold seasons (June–August) (Wirsing *et al*. 2006). Thus, although dolphins are only rarely killed by sharks in the study area, Heithaus and Dill (2002) suspected that they might nevertheless be affected negatively by their predators. Specifically, they hypothesized that individual dolphins might switch between shallow and deep habitats in a threat-sensitive manner, trading the bounty of the shallows for the increased safety offered by impoverished deep channels during periods when sharks are abundant.

Dolphins consume highly mobile prey, which precluded Heithaus and Dill (2002) from using GUDS to index patch-specific patterns of time allocation by foraging individuals. Instead, they applied ideal free distribution (IFD) theory (Fretwell and Lucas 1970). IFD theory predicts that consumers should allocate their time to foraging patches such that all individuals experience the same energy intake rate, or payoff. Under this scenario, the consumer population exploits particular patches in proportion to food supply, and forager densities in all habitats should be equivalent after correction for relative food availability (*e.g.*, division of consumer densities by the amount of food each patch offers). Alternatively, if predation risk influences consumer habitat choice, then individual foragers should allocate more time to safe patches than predicted by food availability alone during periods when defensive investment is necessitated (*e.g.*, when predator numbers are elevated), leading to reduced forager densities in dangerous patches following correction for food supply (van Baalen and Sabelis 1993, Brown and Kotler 2004). Therefore, differences between forager densities for two patch types that emerge when investment in antipredator defense is warranted, and are not explained by spatial variance in food supply, can serve not only to identify the habitat that is perceived to be relatively safe by prey individuals—the spatial pattern, or seascape, of fear—but also as a proxy for the amount of food being sacrificed by foragers electing to avoid dangerous habitat (van Baalen and Sabelis 1993).

Following this framework, Heithaus and Dill (2002) divided the number of foragers in each patch type by habitat-specific levels of fish availability, contrasting the time foraging dolphins allocated to shallow and deep patches during periods of high and low shark abundance. Over a 3-yr period, Heithaus and Dill (2002) found that dolphins consistently allocated their time to shallow and deep foraging patches according to fish availability (*i.e.*, matched their food supply) during the two winters when tiger sharks were scarce (Fig. 1). In contrast, individual dolphins allocated significantly more time to deep habitats than expected based on food supply during

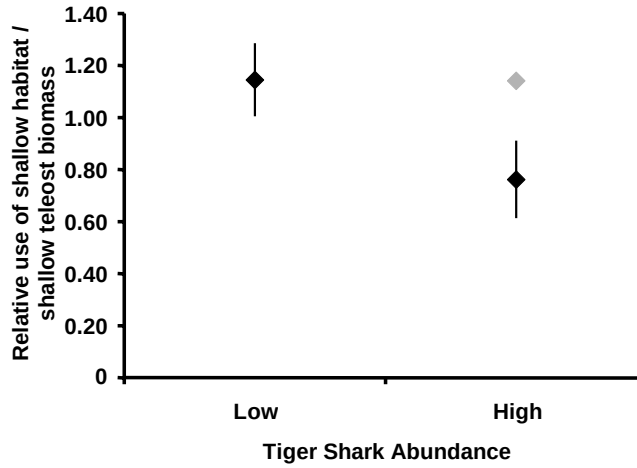

Figure 1. Relative use of shallow (*vs*. deep) habitat by bottlenose dolphins after correction for food supply (teleost biomass) during periods of tiger shark abundance (high) and scarcity (low), means ± SE. A value of 1 signifies equivalent use of the two habitat types after food correction, whereas values <1 represent overuse of deep habitat. The gray diamond indicates the value expected during periods of shark abundance in the absence of a fear effect.

the three summers and one winter when sharks were common (Fig. 1). Based on this "natural experiment," the authors concluded that (1) deep waters are perceived as havens from shark predation by dolphins; (2) dolphins give up food in exchange for safety by shifting from shallow to deep habitats when their predators are abundant; and (3) by inducing dolphins to periodically avoid dangerous shallow patches, tiger sharks may provide a predictable temporal refuge from predation for a variety of fish species that inhabit the shallows and, in so doing, indirectly influence the structure of the Shark Bay sea grass community.

Interestingly, Heithaus and Dill (2006) found that dolphins shifted their foraging locations within shallow habitats (*i.e.*, their microhabitat use) in a threat-sensitive manner as well. Specifically, dolphins foraging in shallow habitats overused the periphery of sea grass meadows (edges), which facilitate escape to safe deep habitat, when sharks were relatively common, and used edge and interior portions of meadows equally relative to the distribution of their prey when sharks were scarce. Tiger sharks prefer to hunt along the periphery of sea grass patches (Heithaus *et al*. 2006). Thus, the authors concluded that, at scales where predator densities and levels of inherent risk are not spatially consistent, bottlenose dolphins seek to avoid being eaten by choosing areas facilitating escape over those where encounters with predators are less likely.

*Case study 2:—Diving by harbor seals (*Phoca vitulina*) in Prince William Sound*—Several pinniped species have been declining in the Northeast Pacific for more than two decades (Springer *et al*. 2003, Trites and Donnelly 2003, Ver Hoef and Frost 2003). The possible link between resource availability and these population declines has motivated foraging studies that search for behavioral signals of bottom-up effects (*e.g.*, Frost *et al*. 2001, Trites and Donnelly 2003). Meanwhile, predators have been considered only as agents of direct mortality that, implicitly, do not influence access to resources (*e.g.*, Springer *et al*. 2003). There is no reason to believe, however, that

Northeast Pacific pinnipeds differ from myriad other species known to compromise energy gain in response to predation risk.

Northeast Pacific pinnipeds overlap spatially with two potential predators: Pacific sleeper sharks (*Somniosus pacificus*) and killer whales (*Orcinus orca*). Predation by killer whales is observable at the surface (*e.g.*, Saulitis *et al*. 2000) whereas interactions between pinnipeds and sleeper sharks might occur in deeper strata, where human observation is difficult. This observational bias has diverted attention from the sublethal effects that intimidation from sleeper sharks might have on pinnipeds (Frid *et al*. 2007*a*).

Frid *et al*. (2007*b*) analyzed behavioral signals that might reflect the relative danger that harbor seals in Prince William Sound experience from different predators. A key feature of the system is that different resources and predator types segregate spatially in the water column. Killer whales hunt at or near the surface, overlapping with Pacific herring *(Clupea pallasi*), whereas sleeper sharks primarily use depths of >100 m (Hulbert *et al*. 2006), overlapping with walleye pollock (*Theragra chalcogramma*). Pollock have lower energy density than herring, and access to them requires longer travel from the surface. However, they also are larger, yielding greater energy content per fish (Trumble *et al*. 2003) and can be encountered much more predictably than herring (Frid *et al*. 2007*b*; and see Litzow *et al*. 2004, Gende and Sigler 2006). Thus, seals might face a complex trade-off when choosing between foraging for herring under risk from killer whales only and pursuing pollock under risk from sharks at depth and from killer whales during surface transitions.

To dissect these trade-offs, Frid *et al*. (2007*b*) predicted net energy gain and predation risk per foraging dive, parameterizing an analytical model with field data on the diving behavior of individual harbor seals, resource distributions, and use of depth by sleeper sharks and killer whales. Analyses suggested that net energetic gain was greatest when seals foraged for pollock in deep strata (>70 m), yet plots of the individuals' predicted energy gain against predicted predation risk fit best when relative danger from sharks was assumed (*via* a model parameter that varied experimentally) to be substantially greater than the relative danger from killer whales. That is, seals underutilized relatively rich resources found in deep strata by reducing the time spent per dive at depths preferred by sleeper sharks, and by reducing the number of dives to those strata (Frid *et al*. 2007*b*; see also Frid *et al*. 2007*a*).

The predicted level of risk-taking associated with this trade-off varied among individuals (Fig. 2). This is unsurprising, given that optimal risk taking should vary according to the individual's residual reproductive value, as influenced by accumulated fat stores, age, and other factors (Lima 1998). Further, overall resource levels should modulate risk taking by the population as a whole (Frid *et al*. 2006 and references within). We can therefore predict, for instance, overfishing of near-surface fatty fishes (*e.g.*, Thomas and Thorne 2003) to make the apparent safety of shallow patches energetically unaffordable, thereby increasing the proportion of seals choosing to forage in deeper and apparently more dangerous strata (Frid *et al*. 2006).

*Case study 3:—Use of alternative foraging tactics by dugongs (*Dugong dugon*) in Shark Bay*—Shark Bay is home to over 10,000 dugongs (Holley *et al*. 2006), many of which make use of our study area (Wirsing *et al*. 2007*b*). These sirenians spend much of their time foraging over Shark Bay's expansive sea grass meadows (>Wirsing *et al*. 2007*b*); while doing so, they can elect to harvest sea grass using one of two primary tactics: cropping, whereby leaves are stripped from the stems of sea grass plants (Anderson 1982), and excavation, whereby individuals dig into the substrate with their rostra to acquire both above-ground and rhizomal portions of sea grass

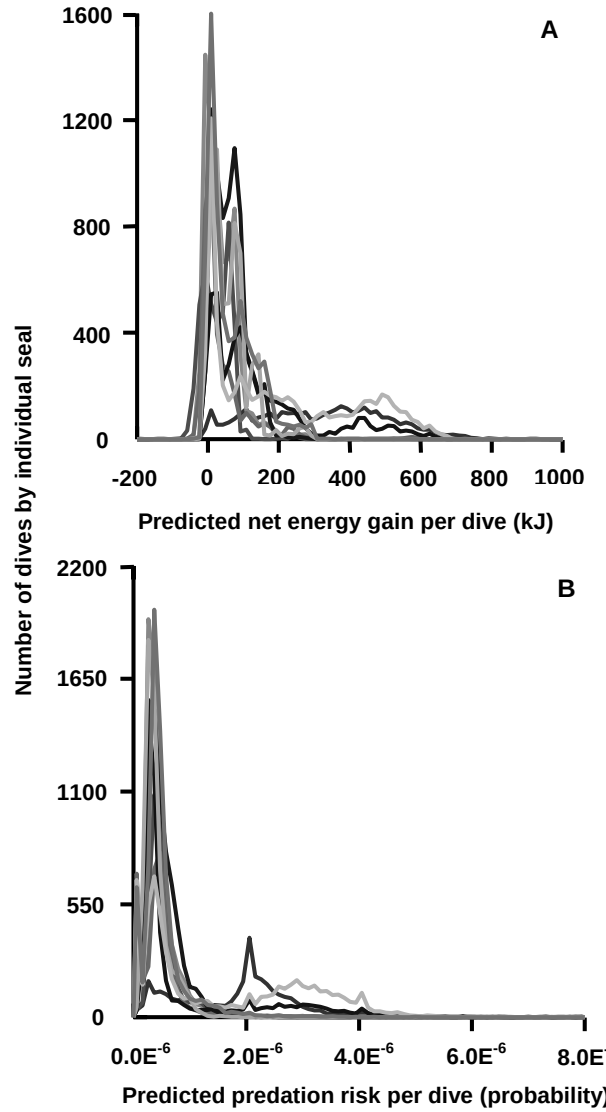

Figure 2. Number of dives performed by individual harbor seals ($n = 9$) to depths associated with different levels of predicted (A) net energy gain and (B) risk of predation. Figure is based on analyses by Frid *et al*. (2007*b*) conjoining empirical data and theoretical simulations, and which predicted positive relationships between diving depth and both net energy gain and predation risk in the Prince William Sound system. Each line represents a different individual.

plants (Anderson and Birtles 1978). In the study area, dugongs crop the temperate sea grass species *Amphibolis antarctica* throughout the year, but excavation is used almost exclusively during the warm season to exploit tropical sea grass species (*e.g.*, *Halodule uninervis*, *Halophila ovalis*) (Wirsing *et al*. 2007*c*). Tropical sea grass species generally are more nutritious than temperate ones (Preen 1995, Masini *et al*. 2001),

so individual dugongs engaging in excavation during the warm season likely achieve higher energy intake rates than conspecifics relying instead on the cropping tactic. However, whereas cropping allows for frequent scans between bites (A. Wirsing, personal observation), the process of excavation entails extended periods of digging that likely preclude vigilance. Furthermore, excavating dugongs often produce huge sediment plumes that may impede surveillance and attract predators. Consequently, dugongs electing to excavate during time periods when both tactics are feasible may pay the cost of increased mortality risk. Accordingly, despite the fact that individual dugongs only rarely succumb to predation, Wirsing *et al*. (2007*c*) suspected that their foraging behavior might nevertheless be affected by predator intimidation. Specifically, they hypothesized that, during the warm season, individual dugongs would switch between cropping and excavation in a threat-sensitive manner, relying on excavation to the lowest degree when tiger shark abundance was highest.

Over the course of four warm seasons, Wirsing *et al*. (2007*c*) observed dramatic changes in the amount of time individual foragers allocated to these two tactics and found that the proportion of foraging time dugongs allocated to excavation was explained well by variation in tiger shark abundance. At the height of each warm season (February–March), when tiger sharks were most abundant, individual dugongs spent very little of their foraging time excavating (<10%), even though levels of tropical sea grass availability also were maximal (Fig. 3). In contrast, the proportion of foraging time dugongs devoted to excavation increased markedly near the tail end of each warm season (April–May), when both shark numbers and levels of tropical sea grass biomass were reduced (Fig. 3). Hence, the authors concluded that dugongs sacrifice much of the nutritional profit they might accrue while excavating sea grass when the high level of apprehension (vigilance) allowed by cropping is required (*i.e.*, when fear of shark predation is high). Given that excavation tends

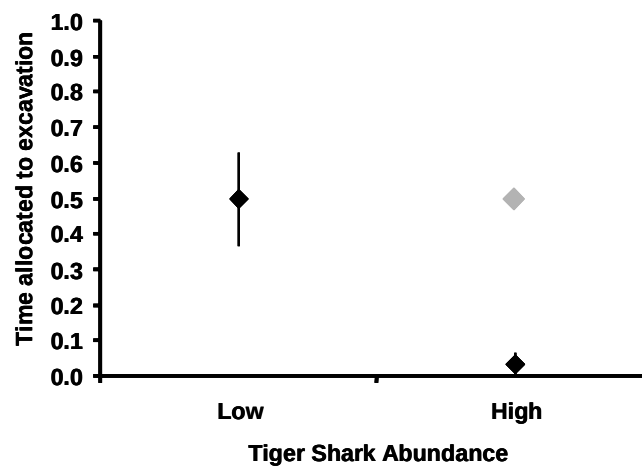

Figure 3. Proportion of time allocated to excavation (*vs*. cropping) by dugongs during the height of the Shark Bay warm season (February–March; high tiger shark abundance) and at the tail end of the warm season (April–May; relatively low shark abundance), means ± SE. The expected value for the former period under the hypothesis of no fear effect is represented by the gray diamond.

to promote sea grass patch succession while cropping facilitates the persistence of perennial sea grass species (Anderson 1986, Preen 1995), Wirsing *et al*. (2007*c*) also speculated that tiger sharks might influence the composition and structure of sea grass meadows indirectly by altering the way they are harvested by dugongs.

Discussion

In their 2001 paper, Laundré *et al*. argue that animals exist in perceptual "landscapes of fear," defined topographically by differing levels of predation risk across space and time. Individual foragers from a variety of taxa have been shown to negotiate these landscapes by avoiding patches perceived to be dangerous, and by allocating more time to apprehension while using patches where risk is high (Lima and Dill 1990, Lima 1998, Brown 1999, Brown and Kotler 2004), yet this paradigm has not often been applied to marine mammals (see George *et al*. 1989 for a speculative example involving bowhead whales, *Balaena mysticetus*). Here, using three case studies involving a cetacean, a pinniped, and a sirenian, we have demonstrated that (1) patterns of time allocation can be used in conjunction with concurrent measures of prey resource and top predator distribution to explore the role of predator intimidation in the lives of large marine vertebrates, and (2) marine mammals, too, are subject to the non consumptive effects of predators and therefore exist in a seascape of fear. In each case, lethal interactions between the focal marine mammal species and its predators were not observed, indicating that predators can dramatically alter the behavior of their marine mammal prey even if they rarely kill them. Note that although all of our examples focus on marine mammals as prey, analogous studies in which the marine mammal plays the role of top predator (*e.g.*, an investigation focusing on the indirect effect exerted by seals on zooplankton *via* trait modification in herring) are equally plausible. We encourage further use of measures of time allocation to address both the intimidation caused and the fear experienced by marine mammals, as information garnered from such investigations should help to foster marine mammal conservation and an improved understanding of the communities of which they are a part.

Many marine mammal populations have been reduced and continue to be threatened by anthropogenic activity, so there is great interest in their conservation (Hofman and Bonner 1985, Anderson 2001). Studies of the time allocation patterns of marine mammals and their prey are likely to facilitate their protection in three ways. First, insofar as the time devoted by prey to safe behavior (*e.g.*, foraging in patches where predation risk is low, vigilance) at any given location is determined in part by the likelihood of encountering predators (*i.e.*, predator density; Brown 1999), spatial measures of the time allocated to antipredator behavior (*vs*. foraging) by animals subject to marine mammal predation can be used to identify marine mammal hotspots. That is, species serving as prey for marine mammals are expected to invest heavily in defense when using areas frequented by their predators, so their antipredator behavior can guide those investigating patterns of marine mammal distribution and help to underpin targeted conservation plans. In contrast, areas featuring prey aggregations should not necessarily be used to identify marine mammal hotspots, as they may serve as refuge habitat where predator (marine mammal) densities, or foraging success rates, are low. Second, time allocation patterns can be employed to identify and categorize critical habitat for marine mammals. For example, relatively high levels of safety-conscious behavior by prey of cetaceans and pinnipeds might be used to

signal areas serving as marine mammal foraging habitat, as prey individuals would not be expected to invest heavily in safety in areas rarely patrolled by their predators. Conversely, relatively low levels of antipredator investment by a given marine mammal species might be used to identify areas it perceives to be either temporary (*e.g.*, seasonal) or permanent havens from predation. To date, difficulties associated with identifying these critical habitats have hampered the creation of marine protected areas that sufficiently address the threats facing marine mammals (Agardy 1994). Third, because animals often perceive human disturbance as a form of predation risk (Frid and Dill 2002), time allocation patterns can serve as an index of the cost imposed by anthropogenic activity on marine mammals in particular areas. For example, a substantial increase in the time devoted to apprehension (or in the use of impoverished refuge habitat) by individual marine mammals following the initiation of an ecotourism program would indicate a potentially costly reduction in foraging time. In contrast, assuming that concomitant changes in resource availability and individual condition have not occurred (see below), a lack of a change in vigilance, as well as in other forms of safety-conscious behavior, would signal an increased likelihood of sustainability.

When a consumer sacrifices food for safety from predators, its resource is often affected indirectly (Werner and Peacor 2003). For example, when dugongs avoid excavating sea grass at the height of the Shark Bay warm season in order to reduce their risk of being eaten by sharks, the sea grass plants they might otherwise harvest are spared, potentially leading to changes in sea grass meadow composition (Case Study 3). Thus, studies of the time allocated to defense by species subject to predation by marine mammals can be used to address the top-down effects marine mammals exert on their communities. Similarly, studies of the time allocation patterns of marine mammal consumers can help determine whether and how they transmit the effects of their predators to more basal trophic levels. In both cases, estimates of the strength of the indirect effect exerted by the apex predator can be generated using the gap between the observed amount of time allocated to foraging behavior by its prey and that expected in the absence of predation danger (*i.e.*, by food availability alone). Conversely, predictions regarding the sign and spatial distribution of the predator's indirect effect on species consumed by its prey will depend on the nature of the prey's time allocation decisions (Schmitz *et al*. 2004). For example, increased use of impoverished refuge patches by an herbivorous marine mammal species in response to fear of predation presumably would benefit plant species in dangerous patches and harm plant species in safe patches. In cases where the potential for strong behavior-mediated indirect effects of top predators on communities is indicated (*i.e.*, where investment in safety by prey is heavy), predictions concerning the spatial distribution of these indirect effects can then guide the design of studies aiming to quantify the impact of defensive adjustments by frightened prey individuals on prey resources. For example, marked variability in prey apprehension across space might serve as a basis for distinguishing specific patch types where measured levels of resource exploitation are likely to differ. The results of these types of studies should in turn lead to an improved understanding of marine community structure.

In closing, we recognize that the environments occupied by marine mammals will usually prevent the calculation of GUDs. Thus, most studies addressing the fear marine mammals experience and generate will necessarily rely on levels of prey apprehension and/or patterns of prey habitat use in the context of IFD theory. For both of these metrics of time allocation, we caution that spatial and temporal correlation between patterns of predation risk and the condition of the prey individuals

or populations under investigation must be taken into account. Otherwise, for example, decreased risk taking elicited by improvements in individual or population energy state may be attributed to fear in the absence of any real predator effect (Lima and Dill 1990, Lima 1998). Moreover, we suggest that these methods will prove most useful in systems where, as in Shark Bay, predation risk is dynamic and, therefore, natural experimentation is possible. In such systems, close correlation between the need for defensive investment (*e.g.*, predator numbers) and the amount of time allocated to defensive behavior over time and across space can be used not only to quantify the effects of fear but also to eliminate the potentially confounding influences of competition among prey individuals and abiotic conditions. In systems where predator numbers are static, conversely, the relative extent to which fear of predation and other factors explain consistent overuse of seemingly safe habitat (or high levels of apprehension in a particular area) may be more difficult to establish.

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