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A comparison of shark and wolf research reveals similar behavioral responses by prey

Aaron J Wirsing[1*] and William J Ripple[2]

Marine and terrestrial ecologists rarely exchange information, yet comparing research from both sides of the land–sea boundary holds great potential for improving our understanding of ecological processes. For example, by comparing the interaction between tiger sharks (*Galeocerdo cuvier*) and dugongs (*Dugong dugon*) to that between gray wolves (*Canis lupus*) and elk (*Cervus elaphus*), we show that top predators in marine and terrestrial ecosystems trigger three similar types of anti-predator behavior: (1) encounter avoidance, (2) escape facilitation, and (3) increased vigilance. By implication, the ecological roles of top predators in both ecosystems may be more similar than previously thought, and studies that fail to account for multiple modes of anti-predator behavior are likely to underestimate these roles and the consequences of eliminating predators from ecosystems. We encourage more communication between marine and terrestrial ecologists, in the interest of generating further insights into ecosystem dynamics and conservation.

A communication gap exists between marine and terrestrial ecologists (Chase 2000). This divide is due in part to the perception that, because of key chemical and physical differences between marine and terrestrial environments (eg the presence or absence of an aquatic medium), many of the ecological processes operating in these two ecosystems are fundamentally different (Steele 1991; Carr *et al.* 2003). This perception is reinforced by compartmentalization within academic institutions and funding agencies (Raffaelli *et al.* 2005; Menge *et al.* 2009). Yet, information sharing across the land–sea boundary has fostered the development and dissemination of many valuable ecological insights, including concepts such as spatial and temporal scales and trophic cascades (Halley 2005; Menge *et al.* 2009; Terborgh and Estes 2010), and helped to answer pressing environmental questions, such as the nature of global carbon cycling (Cole 2005). Thus, where possible, a healthier exchange of information between ecologists working on either side of the marine–terrestrial interface should yield new insights and

general rules that enhance our understanding of each ecosystem, allow for better prediction of ecosystem responses to perturbation, and guide conservation policy (Steele 1991; Chase 2000; Duarte 2007).

Predator risk effects – lost foraging opportunities and reduced growth and reproduction experienced by prey investing in anti-predator behavior – are now widely acknowledged as having important implications for prey populations and ecosystem dynamics (Ripple and Beschta 2004; Schmitz *et al.* 2004; Creel and Christianson 2008; Heithaus *et al.* 2008). However, few studies have compared behavioral responses to predation risk in both marine and terrestrial settings (see Peckarsky *et al.* [2008] for an example), perhaps inhibiting the formulation of general rules governing the nature and ecological consequences of risk effects. Here, we highlight several striking examples of similarities between marine and terrestrial anti-predator behavior, paying special attention to parallels between the behavioral responses of dugongs (*Dugong dugon*) to tiger sharks (*Galeocerdo cuvier*) in the coastal seagrass ecosystem of Shark Bay, Australia, and of elk (*Cervus elaphus*) to gray wolves (*Canis lupus*) in Yellowstone National Park, Wyoming, USA (Figure 1). Our goal is to show how insights can be gained from the "cross-pollination" of ideas from studies in different ecosystems and how this can encourage further communication and collaboration between ecologists tackling similar questions on either side of the land–sea boundary.

■ **Behavioral responses of dugongs to tiger sharks**

Dugongs are large, marine mammalian grazers that inhabit warm, coastal waters throughout the Indo–Pacific region. In Western Australia's Shark Bay, where dugongs number between 10 000 and 14 000 (Gales *et al.* 2004), shallow banks (water depth < 4.5 m) covered by dense

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In a nutshell:

- Traditionally, there has been a communication gap between marine and terrestrial ecologists
- Using gray wolves and tiger sharks as examples, we show that top predators in terrestrial and marine ecosystems trigger similar behavioral responses among respective prey species, suggesting that they play similar ecological roles
- More frequent information exchange between terrestrial and marine ecologists should provide additional insights into our understanding of ecosystems and will help to guide conservation policy

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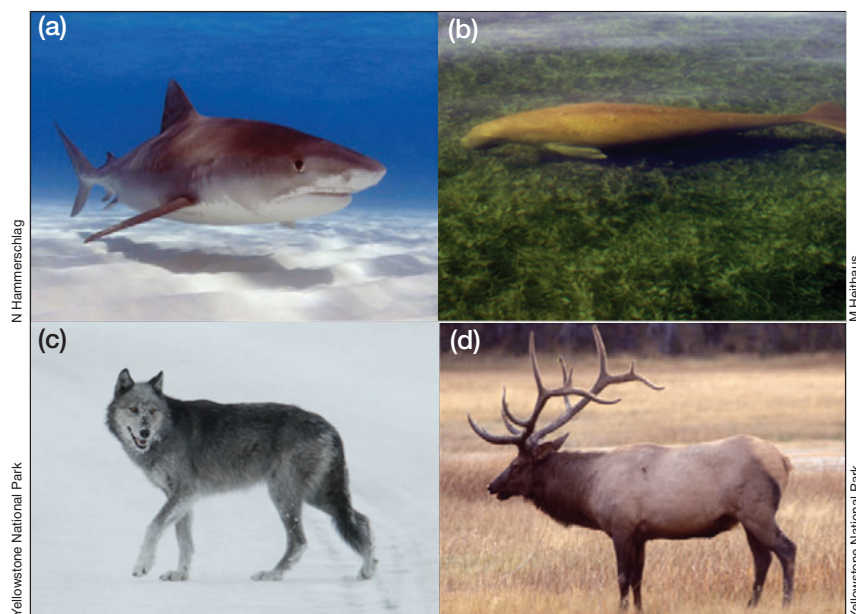
Figure 1. a) Tiger shark (Galeocerdo cuvier); (b) dugong (Dugong dugon); (c) gray wolf (Canis lupus); and (d) elk (Cervus elaphus).

seagrass meadows (predominantly *Amphibolis antarctica*) lie amidst deeper channels (depths >6 m) with sandy substrates. Because they are seagrass specialists, dugongs in this subtropical ecosystem spend the majority of their time foraging in shallow water (Wirsing *et al.* 2007a). However, the strength of this large-scale (hundreds of meters to kilometers) habitat preference is not temporally consistent. Rather, it varies over time because dugongs in Shark Bay must cope with the risk of predation by tiger sharks, which show a preference for shallow banks over deep channels (Heithaus *et al.* 2002) and fluctuate in abundance with seasonal water temperature from a high in February to a low in July (Wirsing *et al.* 2006). When sharks are abundant, dugongs sacrifice food that might otherwise be acquired in shallow waters by increasing their time spent in deeper water, where seagrass is relatively scarce but the encounter rate with sharks is lower (Wirsing *et al.* 2007a; Figure 2a).

Tiger sharks do not hunt shallow seagrass banks uniformly. Instead, they spend more time patrolling peripheral (edges) than internal (interiors) portions of banks (Heithaus *et al.* 2006). Dugongs foraging on shallow banks when sharks are present manifest a surprising small-scale (tens of meters) shift. Namely, they increase their relative use of edges, where encounters with sharks are more likely, and thereby leave behind interior seagrass plants that they might otherwise have harvested (Wirsing *et al.* 2007b; Figure 2b). In doing so, dugongs benefit from an improved ability to escape to the safety of deep channels, where predators are far less numerous and increased water volume confers a maneuverability advantage over attacking sharks (Heithaus *et al.* 2006) that outweighs the cost of additional predator encounters.

Dugongs also alter their fine-scale behavior at foraging locations over shallow banks. When tiger sharks are numerous, dugongs virtually abandon a profitable forag-

ing tactic – excavation – that gives access to relatively nutritious seagrass rhizomes (roots), but inhibits vigilance by requiring a head-down posture. Instead, they switch almost entirely to a less rewarding but safer tactic – cropping – that facilitates head-up surveillance, but only allows for the acquisition of nutrient-poor terminal leaves from seagrass plants (Wirsing *et al.* 2007c; Figure 2c). In other words, dugongs are only willing to take advantage of opportunities to harvest seagrass rhizomes through excavation behavior when there is less need to scan their surroundings for sharks.

■ Behavioral responses of elk to gray wolves

Elk are one of the largest terrestrial mammals in North America. Inhabiting grasslands and forest, these generalist herbivores can function as both grazers and browsers and are the primary prey of gray wolves in the Rocky Mountains of southern Canada and the northern US. Following the reintroduction of wolves into Yellowstone National Park in 1995 and 1996, researchers have documented behavioral effects associated with trophic cascades, whereby elk, under the risk of predation by wolves, alter their habitat use and foraging patterns, vigilance, movements, group size dynamics, and other traits. (Laundré *et al.* 2001; Ripple and Beschta 2004; Creel *et al.* 2005; Hernández and Laundré 2005; Fortin *et al.* 2005). For example, when wolf packs are nearby, Yellowstone elk move from open grasslands – where food quality is highest – to coniferous forest cover, where encounters with wolves are less likely (Creel *et al.* 2005; Figure 2d).

Elk vulnerability to wolf predation is heightened by numerous features of the terrain, including deeply incised channels, multiple channels, oxbows, cut banks, terraces, and woody debris accumulations, each of which may cause fleeing ungulates to lose speed and maneuverability during a chase (Bibikov 1982; Bergman *et al.* 2006; Ripple and Beschta 2006). Accordingly, elk exposed to the risk of predation by wolves have been found to avoid sites near streams, where these impediments are common, at all times of the day and night (Beyer 2006), presumably to improve their ability to escape. Furthermore, after the return of wolves, elk browsing on aspen (*Populus tremuloides*) was found to be lower in the vicinity of downed logs, which could impede fleeing elk (Ripple and Beschta 2007; Figure 2e).

Elk respond to increases in predation risk with correspondingly higher vigilance rates, and this results in reduced foraging time (Laundré *et al.* 2001; Childress and Lung 2003). Thus, high levels of elk vigilance can represent a response to an amplified level of fear and the increased expectation of an attack by predators. Studies

have shown increased average female elk vigilance levels following wolf reintroduction and greater female elk vigilance levels in high wolf-density than in low wolf-density areas (Laundré *et al.* 2001; Childress and Lung 2003). Elk vigilance was also significantly higher near escape impediments (< 30 m) than at locations away from such impediments (Halofsky and Ripple 2008; Figure 2f). This pattern of vigilance has apparently triggered a cascade effect characterized by reduced elk browsing and taller willows (*Salix* sp) and aspen within Yellowstone's valley bottoms, especially where escape impediments occur in relatively close proximity to these woody species (Ripple and Beschta 2006, 2007).

■ Similarity between anti-predator behavior elicited by tiger sharks and wolves

Despite their shared role as top predators, large elasmobranchs (the taxonomic subclass that includes sharks) and canids have not been the subject of comparative studies. Yet, we show that the presence of tiger sharks and wolves sparks an analogous set of anti-predator behaviors in a large marine (dugong) and a large terrestrial (elk) herbivore, respectively. This close match between dugong and elk defensive behaviors suggests that predator risk effects can be transmitted through marine and terrestrial communities in a remarkably similar manner. Furthermore, the magnitude and variety of these behavioral responses underscore the strong potential for anti-predator behavior to influence patterns of prey distribution and foraging in both ecosystems, even if the intensity of predator-induced mortality (ie direct predation) is low. Anti-predator responses by dugongs and elk lie along at least three behavioral axes, corresponding to different spatial scales (Figure 2). At the largest spatial scale, both herbivores apparently shift habitats to avoid encounters with predators when exposed to risk, with dugongs decreasing their use of shallow banks where sharks are abundant in favor of deeper water and elk moving away from open grasslands that are monitored by wolves and into the protective cover of coniferous woodlands. At an intermediate spatial scale, both prey species altered their foraging location to facilitate escape from would-be attackers, when using areas where encounters with predators were likely. Specifically, with sharks present, dugongs foraging over shallow seagrass banks increased their use of peripheral locations (edges), which provide for increased maneuver-
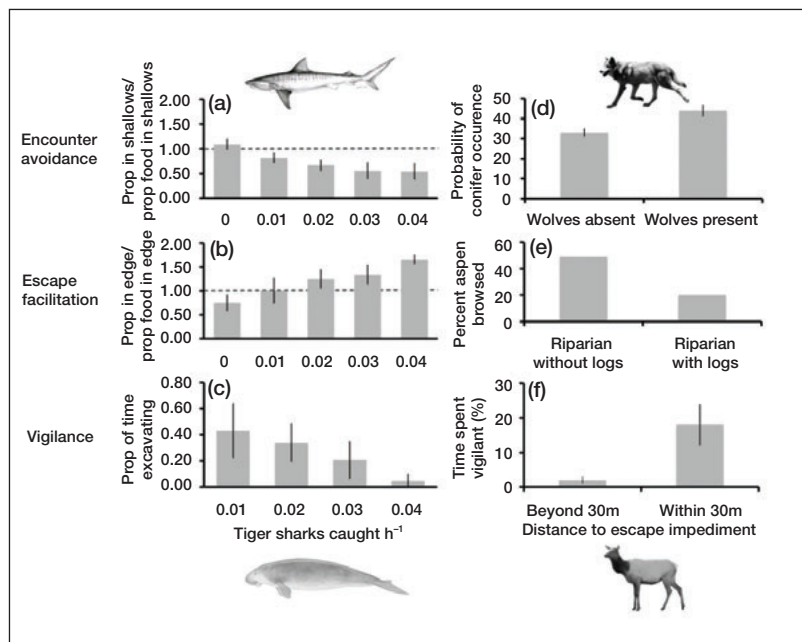

Figure 2. Manifold risk effects of tiger sharks on dugongs and gray wolves on elk. (a) As relative shark abundance (catch rate h^{-1}) increases, the proportion (prop) of dugongs foraging over shallow seagrass meadows decreases successively more than expected, based on the proportion of food (seagrass) in the shallows (dashed black line), indicating a predator-induced shift into deeper water where encounters with sharks are less likely. (Adapted from Wirsing et al. 2007a.) (b) With rising shark abundance, the proportion of foraging dugongs along the edges of shallow seagrass meadows begins to exceed that expected, based on the proportion of food at the edges (dashed black line), indicating a shift from interior portions of meadows to peripheral areas, where the probability of escape into deep water is elevated. (Adapted from Wirsing et al. 2007b.) (c) The proportion of time dugongs devote to excavation, a foraging tactic that inhibits vigilance, declines as tiger shark abundance increases. (Adapted from Wirsing et al. 2007c.) (d) When wolves are present, elk often shift from open grasslands to conifer forests (ie probability of conifer occurrence at locations of elk with GPS collars increases), possibly to decrease encounters with wolves. (Adapted from Creel et al. 2005.) (e) Elk browse more aspen at sites without downed logs (escape impediments), likely to enhance escape possibilities in case of wolf attack. (Adapted from Ripple and Beschta 2007.) (f) Elk vigilance is highest near escape impediments, likely in response to enhanced vulnerability to wolf predation. (Adapted from Halofsky and Ripple 2008.) In (a)-(d), bars show means and 95% confidence interval. In (f), bars show means and standard error.

ability and easy access to deep water. Similarly, while using areas patrolled by wolves, elk concentrated their foraging at locations away from escape impediments (eg downed logs). At a fine spatial scale (the foraging location), both herbivores apparently invest more heavily in vigilance when under increased threat of predation, with dugongs increasing their use of a foraging tactic – cropping – that enables more effective surveillance when sharks are abundant and elk increasing their use of a watchful, head-up posture when feeding near obstacles that could impede their escape. More anti-predator behavioral parallels not considered in this paper are possible; for example, elk adjust their group dynamics in response to wolf predation risk (Winnie and Creel 2007),

and dugongs responding to tiger sharks may do so as well. By implication, anti-predator responses by prey in both marine and terrestrial environments can be complex, meaning that studies in either domain that neglect one or more of the kinds of responses documented here are likely to underestimate or fail to detect risk effects and, as a result, result in an incomplete understanding of the roles played by predators in ecological communities.

The multiple types of anti-predator behavior exhibited by dugongs and elk suggest that predators may indirectly affect species that serve as food for their prey (typically producers like plants, but also smaller consumers if the prey species is a carnivore) via diverse and sometimes conflicting pathways (Figure 3). That is, behavioral responses, such as encounter avoidance and enhanced vigilance, would be expected to benefit producers in areas where predators are abundant by displacing or reducing the time devoted to foraging by prey. In contrast, efforts by prey to improve their chances of escape could lead to either diminished or heightened exploitation of producers, where predators are relatively numerous, depending on the degree of spatial correlation between predator abundance and the ability of the prey species to escape attack. In Shark Bay, for example, shifts into deep water (encounter avoidance) and increased reliance on cropping (investment in vigilance) by dugongs responding to tiger sharks likely benefit shallow seagrass meadows by reducing both the number of foragers and the extent to which seagrass plants are destroyed by excavation. On the other hand, heavy use of edges (escape facilitation) by dugongs under threat of predation has mixed consequences for seagrass meadows, diminishing pressure on interior seagrass plants but intensifying herbivory along the meadow periphery (Heithaus *et al.* 2007).

In general, the net response of a prey individual to a predator is the product of several modes of behavioral adjustment. When these modes of adjustment have different consequences for producers, the overall nature of a predator's indirect effect on any particular producer (ie positive or negative) should be contingent upon their relative magnitude. Accordingly, we suggest that studies that compare the strength of multiple types of prey anti-predator responses may facilitate prediction of whether producers subject to the indirect effects of predators are winners or losers (Schmitz *et al.* 2000).

◼ Other examples of similarity between marine and terrestrial anti-predator behavior

Many other features of anti-predator behavior also appear to transcend the land–sea boundary. Here, we discuss three that should serve as a basis for fruitful exchange between marine and terrestrial ecologists: (1) the dependence of anti-predator behavior on prey body condition or energetic state; (2) the dependence of anti-predator behavior on prey escape mode; and (3) the influence of such behavior on community properties relative to that of

consumptive predator effects (ie reduction of prey density via direct predation). Each of the following three sections compares a pair of case studies drawn from the marine and terrestrial literature to demonstrate the generality of one of these features.

Prey body condition (energetic state)

Studies from marine and terrestrial systems reveal an analogous relationship between prey body condition, or energetic state, and investment in anti-predator behavior. In Shark Bay, for example, green sea turtles (*Chelonia mydas*) at risk of predation by tiger sharks invest more heavily in anti-predator behavior (ie take fewer risks) as their body condition improves, spending more time foraging along the perimeter of seagrass meadows, where the quality of the plants on which they rely is reduced but escape to deeper water is easier (Heithaus *et al.* 2007). Similarly, common wildebeest (*Connochaetes taurinus*) under threat from lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) on the African Serengeti take greater risks when in poor condition and, as a result, succumb to predation more often than individuals in better condition (Sinclair and Arcese 1995). By implication, risk effects in both marine and terrestrial ecosystems probably work synergistically with direct predation and bottom-up forces (eg food supply) to control some prey populations, with reductions in resources triggering elevated risk-taking by energetically stressed prey individuals, heightened predation rates, and, ultimately, prey population declines (McNamara and Houston 1987; Heithaus *et al.* 2008). Exchanges between marine and terrestrial ecologists exploring responses to predators by prey with varying body condition (ie condition-dependent risk-taking) should facilitate a more general understanding of this synergistic process.

Prey escape mode

Behavioral responses to predators are also contingent on prey escape mode in both marine and terrestrial ecosystems (Wirsing *et al.* 2010). For example, like dugongs and healthy green turtles, Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in Shark Bay shift toward the periphery of shallow seagrass meadows – where their escape mode (maneuvers and rapid movement into deeper water) is facilitated – when exposed to tiger shark predation risk (Heithaus *et al.* 2009). Pied cormorants (*Phalacrocorax varius*) in this system, on the other hand, fly away from sharks and therefore cannot improve their chances of escape by foraging in close proximity to deep water. Thus, they spend more time near the center of seagrass meadows, where encounters with sharks are less likely, when exposed to risk (Heithaus *et al.* 2009). Similarly, two sympatric prairie ungulates (white-tailed deer, *Odocoileus virginianus*, and mule deer, *Odocoileus hemionus*) in southern Alberta, Canada, show divergent spatial shifts when exposed to coyote (*Canis latrans*) predation risk that are explained well by differences in their escape tactics (Lingle 2002).

Specifically, white-tailed deer, which flee to escape predation, increase their use of gentle terrain that allows for maximum speed, whereas mule deer, which are slower and actively defend themselves against predators, shift onto sloped, rougher terrain where coyotes are unlikely to give chase. Thus, in many systems, the nature of the indirect effect of a predator on producers (ie negative or positive) may depend in part on the escape tactic of the prey species. On open prairie terrain in Alberta, for instance, the presence of coyotes probably provides a reprieve for plants consumed by mule deer, while enhancing the intensity of herbivory by white-tailed deer. Clearly, further exchanges between marine and terrestrial ecologists will help to resolve the generality of escape behavior as a driver of variability in the effects of predation risk on sympatric prey species and producers.

Indirect influence of predator risk effects

Studies in both marine and terrestrial ecosystems reveal that the indirect influence of predator risk effects in communities can rival or exceed that of the consumptive effects of direct predation. For example, in a rocky intertidal system, Trussell *et al.* (2006) showed that the risk posed by predatory green crabs (*Carcinus maenas*) induced behavioral changes in an intermediate consumer (ie reduced rate of foraging and increased refuge use by the carnivorous gastropod *Nucella lapillus*), which in turn precipitated a marked (580%) increase in the abundance of a basal resource (the acorn barnacle, *Semibalanus balanoides*). This risk effect represented the majority (86%) of the total indirect effect (ie behavioral modification plus direct predation) of green crabs on barnacles in areas where barnacles are subject to predation by snails. Similarly, in a New England old-field ecosystem, Schmitz (1998) found that the presence of "risk spiders" (ie *Pisaurina mira* individuals with their mouthparts experimentally altered so they could not feed) induced a diet shift in a herbivorous grasshopper (*Melanoplus femurrubrum*) that in turn altered plant community characteristics (diversity and productivity). Replacement of these "risk spiders" with "predation spiders" capable of killing prey did not alter grasshopper density and had no measurable effect on this indirect relationship, suggesting that it was driven entirely by changes in prey behavior (ie a risk effect).

■ Conclusions

Predator risk effects have long been a popular topic of study and are now widely recognized as an important structuring process in ecological communities (Werner
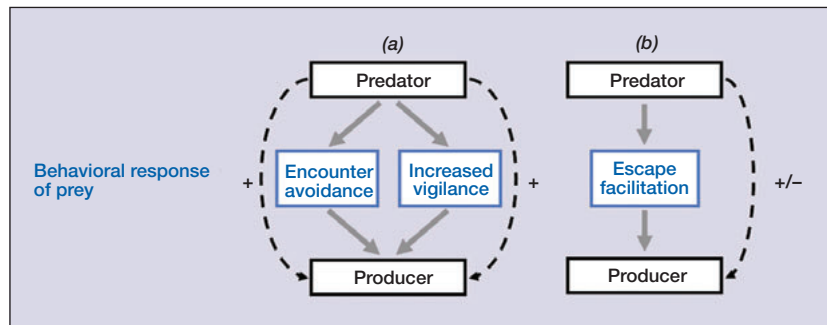

Figure 3. Conceptual model of potential trophic cascades, showing indirect effects of a predator (dashed arrows) on a producer (eg a plant) that are transmitted by three different types of prey anti-predator behavior (highlighted in blue). Gray arrows signify direct effects, including predator-induced behavioral adjustments by prey and changes in foraging pressure imposed by prey on producers. In a landscape where hunting pressure by a predator species varies spatially, heavy hunting activity in any particular area could indirectly benefit producers by eliciting encounter avoidance and increased vigilance (a) and, as a result, reduced foraging by prey. Selection for areas facilitating escape by prey, however, could either increase or decrease prey density and foraging intensity in heavily hunted areas, depending on the degree of spatial correlation between predator hunting activity and the effectiveness of the prey's escape tactic. Consequently, the indirect effect of a predator on producers in heavily hunted areas that is transmitted by prey escape facilitation may be positive or negative (b). The net indirect impact of a predator on producers in areas with high predator hunting activity is a function of the relative strength and interaction of these three types of prey behavioral responses.

and Peacor 2003; Ripple and Beschta 2004; Schmitz *et al.* 2004; Preisser *et al.* 2005; Wirsing *et al.* 2008), but our understanding of the factors governing their strength and nature in particular cases remains incomplete (Creel and Christianson 2008; Heithaus *et al.* 2008). An improved understanding of risk effects is crucial if we are to better explain the organization of communities and more reliably predict the consequences of predator loss or restoration for ecosystem dynamics.

Our comparison of anti-predator behavior evoked by tiger sharks and gray wolves reveals that prey behavioral responses to danger can fall along multiple axes (encounter avoidance, escape facilitation, increased vigilance), irrespective of ecosystem. Evidence from other studies suggests that these three behavioral axes may characterize the anti-predator responses of prey in a wide variety of systems. For example, bottlenose dolphins in Shark Bay not only facilitate their probability of escape by foraging along the perimeter of seagrass meadows, as mentioned above, but also avoid encountering tiger sharks by using deep water (Heithaus and Dill 2002) and reduce their use of a foraging tactic than inhibits vigilance (bottom grubbing; Sargeant *et al.* 2007) when at risk. Similarly, redshanks (*Tringa totanus*) generally avoid their predators but employ flocking and vigilance to enhance their probability of escape and detecting an attack, respectively, when exposed to the threat of predation (Cresswell 1994; Sansom *et al.* 2009). By implication, failure to account for the multifaceted nature of anti-predator behavior could lead to an underestimation

of the role of risk effects, erroneous conclusions about the consequences of changes to predator populations for ecosystem properties, and an increased likelihood of mismanagement. We therefore recommend that studies of risk effects should feature a design capable of capturing multiple forms of anti-predator behavior.

Thus far, we have sought to highlight the value of "cross-pollinating" studies of risk effects in marine and terrestrial systems. Importantly, a communication gap exists between ecologists working in these two ecosystems and those exploring freshwater aquatic systems as well (Menge *et al.* 2009). Given the seminal work that has been conducted on risk effects in freshwater environments (eg Peacor and Werner 2001), we suggest that efforts to bridge this divide should also promote an improved understanding of risk effects and more effective predator conservation.

Finally, there are many other themes on which either marine or terrestrial ecologists continue to focus heavily and that have general applicability. For example, marine ecologists have advanced our understanding of whole-ecosystem dynamics with trophic (feeding) network analyses that are little used by their terrestrial counterparts (Raffaelli *et al.* 2005). Terrestrial ecologists have advanced our understanding of the relationship between species diversity and ecosystem properties to a greater extent than have marine ecologists (Raffaelli *et al.* 2005). We hope that the comparative exercise presented here will promote increased communication between marine and terrestrial researchers studying these and other topics that transcend ecosystem boundaries.

■ Acknowledgments

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