

Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics

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Summary

1. Risk effects of predators can profoundly affect community dynamics, but the nature of these effects is context dependent.
2. Although context dependence has hindered the development of a general framework for predicting the nature and extent of risk effects, recent studies suggest that such a framework is attainable if the factors that shape anti-predator behaviour, and its effectiveness, in natural communities are well understood.
3. One of these factors, the interaction of prey escape tactics and landscape features, has been largely overlooked.
4. We tested whether this interaction gives rise to interspecific variation in habitat-use patterns of sympatric large marine vertebrates at risk of tiger shark (*Galeocerdo cuvier* Peron and LeSueur, 1822) predation. Specifically, we tested the a priori hypothesis that pied cormorants (*Phalacrocorax varius* Gmelin, 1789) would modify their use of shallow seagrass habitats in a manner opposite to that of previously studied dolphins (*Tursiops aduncus* Ehrenberg, 1833), dugongs (*Dugong dugon* Müller, 1776), and green turtles (*Chelonia mydas* Linnaeus, 1758) because, unlike these species, the effectiveness of cormorant escape behaviour does not vary spatially.
5. As predicted, cormorants used interior and edge portions of banks proportional to the abundance of their potential prey when sharks were absent but shifted to interior portions of banks to minimize encounters with tiger sharks as predation risk increased. Other shark prey, however, shift to edge microhabitats when shark densities increase to take advantage of easier escape despite higher encounter rates with sharks.
6. The interaction of landscape features and escape ability likely is important in diverse communities.
7. When escape probabilities are high in habitats with high predator density, risk effects of predators can reverse the direction of commonly assumed indirect effects of top predators.
8. The interaction between landscape features and prey escape tactics can result in a single predator species having differential effects on their sympatric prey that could cascade through ecosystems and should be incorporated into a general framework for context dependence of risk effects.

Key-words: anti-predator behaviour, community dynamics, nonconsumptive effects, seagrass ecosystem, top-down effects, tiger shark, trait-mediated indirect interactions (TMII)

Introduction

Predators affect their prey through both direct predation and risk effects (or nonconsumptive effects) that may cascade through communities (e.g. Preisser, Bolnick & Bernard 2005;

Creel & Christianson 2008). Increasingly, however, ecologists are recognizing that risk effects, which often result when prey exchange foraging opportunities for increased safety, and their resulting behaviourally mediated indirect species interactions are context dependent (Schmitz 2008) and that understanding the natural history details of predator–prey interactions is important for predicting community dynamics.

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For example, specific hunting modes of sympatric predatory spiders (sit-in-wait vs. roving) have opposite indirect effects on plant communities because they induce divergent anti-predator responses by foraging grasshoppers (Schmitz 2008), showing that predators foraging for shared prey in the same landscape but with different tactics can have differential impacts on the wider community. Less appreciated is the possibility that the indirect effects of a single predator, using one foraging mode, could be contingent on the interaction of prey anti-predator behaviour and landscape features (Schmitz 2007). What remains uncertain is the mechanism by which the contingent responses arise. Our purpose here is to offer some insight into the way risk responses of prey to predators could lead to contingent outcomes on community structure and dynamics.

Predation risk can be decomposed into two components – the probability that a prey individual encounters a predator and the probability that the prey is killed as a result of that encounter (Lima 1992, Hugie & Dill 1994). In many cases, encounter probabilities are likely to be proportional to the abundance of predators in a habitat (but see Mills 1990; Brown & Brown 1996; Creel & Creel 2002 for exceptions). What must be resolved more clearly is the conditional probability of prey death (which includes the probability that prey are attacked when encountered and are able to escape if attacked; see Creel & Creel 2002) and how prey weight encounter probabilities against their conditional probability of death. This understanding has important implications for predicting the dynamics of communities and for ecosystem conservation. For example, if only encounter rates with predators drive anti-predator decisions, then prey should attempt to avoid areas of high predator abundance and such anti-predator behaviour should amplify the effects of direct predation in habitats with high predator abundance, resulting in reduced exploitation of the resources of prey. Conversely, if prey select habitats based primarily on the conditional probability of death in an encounter situation (e.g. early detection, habitat-specific escape ability or habitat-specific predator lethality), then habitat attributes that increase safety or susceptibility to predators, rather than those predictive of predator abundance, should be stressed in community models and conservation practices. This is because of the counterintuitive proposition that if predators are concentrated in areas where conditional probabilities of prey death are *low*, prey should congregate in areas with *high* predator abundance because their overall probability of being killed by a predator may be lower there. Habitat shifts of this type have been little studied (but see Lima 1992 for a theoretical treatment) and are of great interest because they would result in a reversal of the sign of indirect interactions between predators and basal resources relative to that predicted by traditional views of predator–prey dynamics (i.e. that predator effects occur only through lethal mechanisms or that prey will always tend to abandon areas with high predator densities). While it may seem unlikely that predators would congregate in habitats where conditional probabilities of prey death (i.e. attack success) are low, such a situation may arise

for generalist predators with access to many prey types that vary in both their abundance and susceptibility to attack across habitats (e.g. Heithaus 2001a) because predators will select habitats based on their overall rate of energy intake rather than that derived from individual prey types.

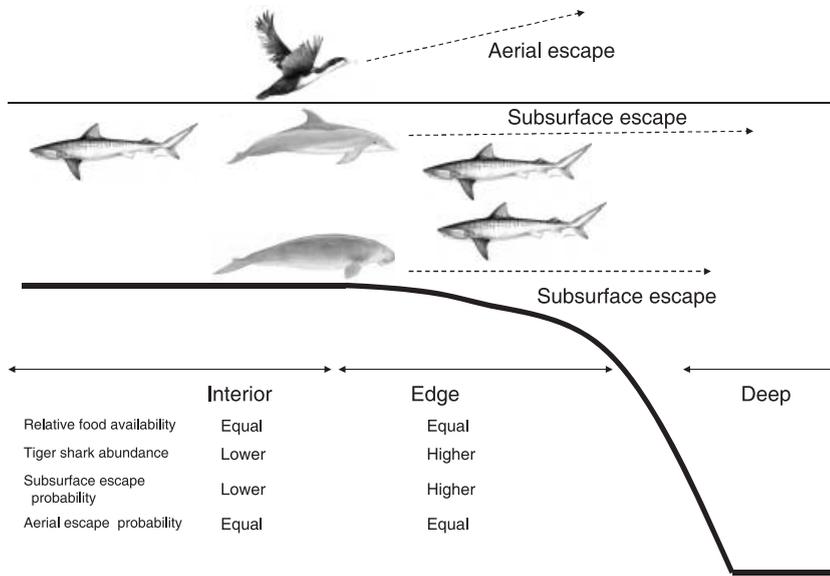
Most studies of predator–prey interactions, especially those involving risk effects of predators and behaviour (or trait)-mediated indirect interactions, focus on single predator and prey species or multiple predators that threaten a single prey species. Yet in order to understand contingent responses, we need to compare how different prey with different habitat or resource needs respond to the same predator species and associated risk within the same landscape rather than assuming that interactions between single predators and single prey species can be generalized to the level of communities. We present here a case study of such a system to illustrate how predation risk-dependent spatial shifts by prey depends on both physical features of their habitat and their particular escape tactics.

The study system

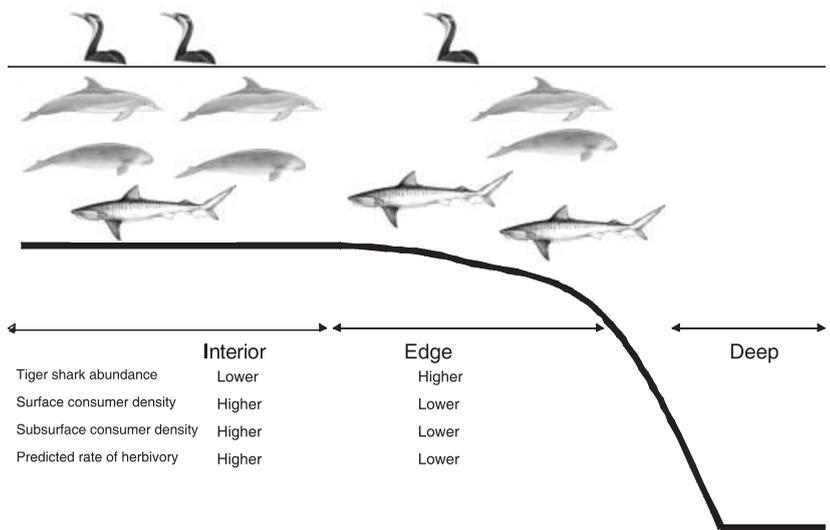
The relatively pristine seagrass community of Shark Bay, Western Australia (ca. 25°45' S, 113°44' E), provides an opportunity to assess the possibility that escape tactics and habitat attributes interact to structure nonconsumptive predator effects in communities. In Shark Bay, tiger sharks (*Galeocerdo cuvier*) are the sole predator for many large marine vertebrates including piscivorous bottlenose dolphins (*Tursiops aduncus*) and pied cormorants (*Phalacrocorax varius*) as well as herbivorous dugongs (*Dugong dugon*) and green turtles (*Chelonia mydas*) (Heithaus 2001b, 2005; Wirsing, Heithaus & Dill 2007a). These species occupy a heterogeneous landscape composed of habitat patches that vary in the abundance of resources (teleosts or seagrass) and predation risk from tiger sharks (Fig. 1). At the broadest spatial scale, the study area can be divided into offshore banks that contain substantial teleost and seagrass resources (1.5–4.5 m depth) and surrounding deeper waters (6–12 m) that are largely unvegetated and support much lower teleost biomass (Heithaus 2004, 2005). Shallow banks can be divided into two microhabitats based on their water depth and distance from deep waters. Interior microhabitats are more than 75 m from the 4.5-m isobath and are less than 2.5 m in depth. Edge microhabitats are 2.5–4.5 m depth or shallower and within 75 m of the 4.5-m isobath. These microhabitats contain similar densities of dolphin prey and seagrass resources for dugongs and sea turtles (Heithaus & Dill 2006; Wirsing Heithaus & Dill 2007b). Interior microhabitats, however, contain more nutritious seagrasses (Heithaus *et al.* 2007).

Tiger shark abundance varies temporally, with numbers at peak periods vastly exceeding those during periods of scarcity (Heithaus 2001c; Wirsing, Heithaus & Dill 2006), and spatially, with shark use (and thus encounter rates with their prey) being highest in shallow edge microhabitats followed by shallow interiors and then deep habitats (Heithaus *et al.* 2006). During an encounter with a tiger shark, dolphins,

(a) Mesoconsumer microhabitat decisions



(b) Lethal effects/encounter rate minimization



(c) Escape probability and encounter rates

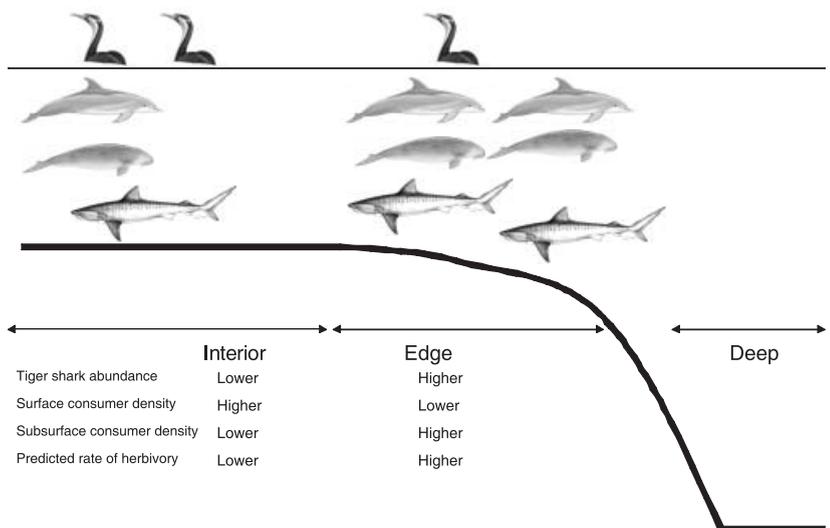


Fig. 1. Schematic representation of microhabitat use decisions of pied cormorants, dugongs, and Indian Ocean bottlenose dolphins at risk from tiger sharks while foraging over shallow seagrass banks. (a) When present, tiger sharks are more abundant in edge microhabitats than interior ones. Cormorants can escape by flying away while dugongs and dolphins must make a subsurface escape to safer deep waters or outmaneuver the shark. (b) If all prey species attempt only to minimize encounters with sharks, they should all be in greater densities in interior microhabitats – a prediction identical to that if lethal effects of tiger sharks were considered. (c) Hypothesized distributions of tiger shark prey incorporating encounter rates and species-specific escape tactics. Because shifting to edge microhabitats can increase escape probabilities for dugongs and dolphins, but not cormorants, the former should preferentially use edge microhabitats despite higher shark abundance while cormorants should minimize encounters.

dugongs, and green turtles flee to safer deep habitats and use their superior maneuverability in three dimensions to avoid being captured by a tiger shark (Heithaus & Dill 2006; Heithaus *et al.* 2007; Wirsing *et al.* 2007a). Thus, these prey species enhance their escape probabilities by moving closer to deep habitats and spending time in areas that allow greater three dimensional maneuverability (i.e. greater water depth) despite higher encounter rates with tiger sharks (Heithaus & Dill 2006; Heithaus *et al.* 2007; Wirsing *et al.* 2007b). In contrast, cormorants fly away when threatened and cannot greatly modify their probability of escaping from a tiger shark by changing their habitat use relative to underwater landscape features (Fig. 1). Based on temporal and spatial variation in tiger shark encounter rates, variation in anti-predator tactics, and the distribution of food resources, we predicted that, unlike other prey species that favour microhabitats with enhanced escape abilities at a cost of higher predator encounter rates, cormorants should shift from using microhabitats proportional to prey abundance when sharks are scarce towards intensive use of the middle of seagrass banks, where shark abundance is lower, when sharks are abundant in the study area (Fig. 1).

Methods

From March to August 2006, we conducted 175 passes along paired transects (3–4 km) representing interior and edge microhabitats of four shallow banks separated from one another by deep channels. We recorded all cormorants at the surface within 30 m of the vessel, which was driven at 6–9 km h⁻¹. All cormorants that fled from the boat upon approach were watched until they landed or left the study zone to avoid counting an individual more than once.

The biomass of cormorant prey (teleosts) was assessed using data from ~1.1 × 0.6 × 0.6 m Antillean-Z fish traps set on all banks (see Heithaus 2004). Briefly, each sampling day, up to five traps were set in each of the two microhabitats concurrently. Traps were baited with approximately 250 g of cut pilchards (*Sardinops neopilchardus*) and allowed to soak for 2 h. When traps were recovered, the fork length of each fish was measured and species-specific length–weight relationships (Heithaus 2004) were used to determine overall catch biomass. Biomass available to cormorants was calculated using all species except those that are toxic and those over 20 cm fork length that are likely to be too large for cormorants to consume (Heithaus 2005). Biomass captured in traps was log ($x + 1$) transformed to normalize data.

We assessed the overall abundance of tiger sharks in the bay using monthly catch rates on drumlines (see Heithaus 2001c; Wirsing *et al.* 2006 for methods), which are a reliable index of tiger shark abundance in the bay (Heithaus 2001c). Tiger shark habitat and microhabitat use have been studied previously and shown to be temporally stable (Heithaus *et al.* 2006).

For every month of the study, we calculated the proportional use of microhabitats by cormorants in relation to the distribution of their potential prey. This was carried out by dividing the density of cormorants (birds per square kilometre) in the edge transect of a bank by the sum of cormorant densities in edge and interior transects of that bank. This value was then divided by the proportion of biomass of potential prey in the edge microhabitats, which was calculated in the same manner (mean biomass per trap in the edge microhabitat of a shallow bank divided by the sum of mean

biomasses in edge and interior microhabitats of that bank). A value of 1.0 indicates that cormorants use edge and interior microhabitats proportional to prey abundance (an ideal free distribution), while values below 1.0 indicate use of interior habitats to a greater extent than expected based on the distribution of food and values above 1.0 indicate overuse of edge microhabitats. We used ANOVA to determine the effects of shark presence, bank identity, and their interaction on the relative use of microhabitats by cormorants in relation to food distribution. Data were not transformed because they were normally distributed (Shapiro–Wilks $W = 0.96$, $P = 0.67$). Nonsignificant ($P > 0.10$) interactions and factors were removed from the final model.

Results

The biomass of cormorant prey did not vary significantly among banks ($F_{3,206} = 1.4$, $P = 0.23$), with shark catch rate ($F_{2,206} = 0.2$, $P = 0.84$), between edge and interior microhabitats ($F_{1,206} = 0.05$, $P = 0.82$) or with an interaction of shark catch rates and microhabitat ($F_{2,206} = 0.8$, $P = 0.43$). There was, however, a slight tendency for higher biomass within interior microhabitats across all shark catch rates. Our measure of relative microhabitat use by cormorants accounted for this possible spatial variation in food abundance. Assuming equal availability across microhabitats, however, does not modify our results because the proportion of fish biomass in each habitat did not vary with shark catch rate (Fig. 2).

As predicted, cormorants used interior and edge microhabitats of shallow seagrass banks approximately in proportion to fish abundance when tiger shark abundance was low.

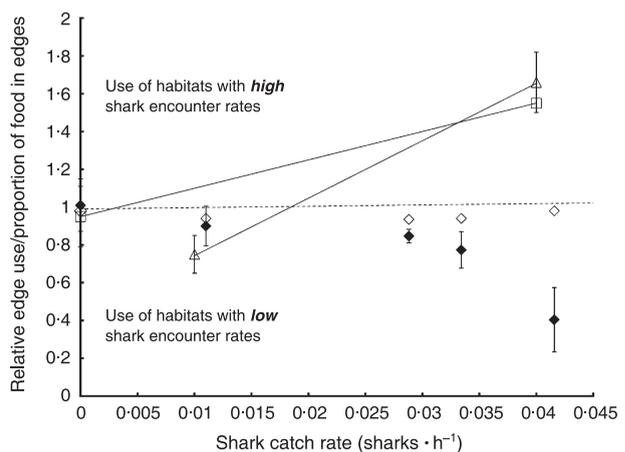


Fig. 2. Responses of dolphins (open squares), dugongs (open triangles), and cormorants (closed diamonds) to increases in tiger shark abundance. Units are the relative use of edge microhabitats divided by the relative availability of food in edge microhabitats. The proportion of potential cormorant prey biomass in edge microhabitats is shown with open diamonds. Cormorants use edge and interior microhabitats in proportion to the abundance of prey in each when shark catch rates are low (i.e. they conform to an ideal free distribution). As shark abundance increases, cormorants switch to using interior microhabitats, where tiger sharks are less common, more often than expected by the distribution of their food. Dolphins and dugongs, however, make the opposite shift – using edge microhabitats more often than expected by food availability when tiger sharks are present. Data from dolphins and dugongs after Heithaus and Dill (2006) and Wirsing *et al.* (2007b), respectively.

Moreover, when tiger shark abundance increased, cormorants reduced their use of edge microhabitats (where tiger sharks are most abundant) and increased their use of interior microhabitats (where tiger sharks are less abundant) relative to that predicted by the availability of fish (microhabitat \times shark abundance: $F_{1,14} = 7.3$, $P = 0.02$; Fig. 2).

Discussion

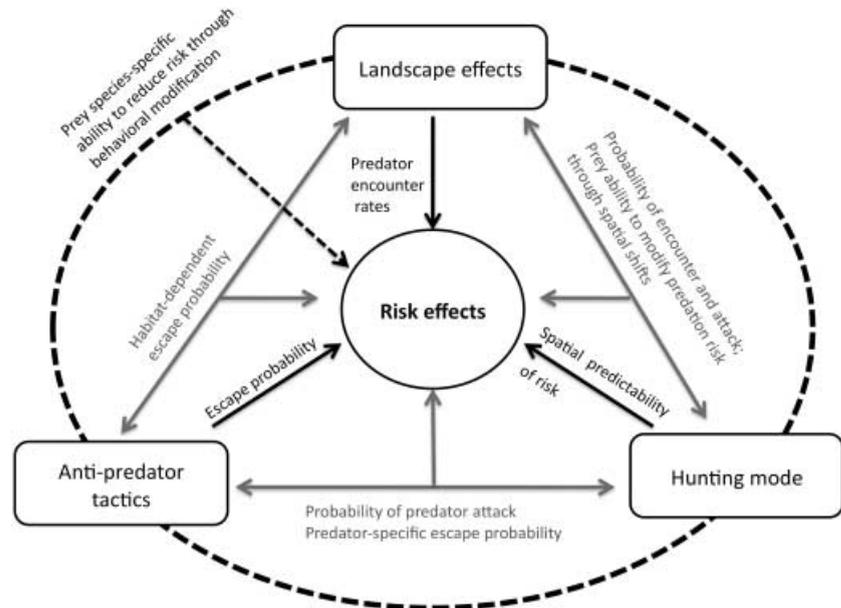
Pied cormorants in Shark Bay respond to tiger shark predation risk by modifying their use of habitats at multiple spatial scales. Like dolphins and dugongs, fewer cormorants make use of prey-rich shallow banks, where tiger sharks are abundant, and more use safer deep habitats, where prey is less abundant, as the overall abundance of tiger sharks increases in the study area (Heithaus 2005; Heithaus & Dill 2006; Wirsing *et al.* 2007a). For those prey individuals using shallow banks, however, there is marked interspecific variation in microhabitat shifts in response to tiger shark predation risk that appears to be driven by how landscape features – in this case water depth and distance from deep water – interact with prey escape tactics to modify overall levels of predation risk within a microhabitat. For cormorants, the probability of avoiding a tiger shark attack during an encounter by flying away is unlikely to vary with microhabitat. Thus, cormorants respond to increasing tiger shark abundance in the study area by shifting from the edges of banks, where tiger shark encounters are most frequent, to interior microhabitats where tiger shark encounters are less common. As a consequence, the behavioural shift by cormorants in combination with higher predation rates by tiger sharks should lead to reductions in cormorant exploitation of fish in edge microhabitats and, in turn, a positive indirect effect of tiger shark presence on cormorant prey; i.e. the indirect risk effect of tiger sharks that is transmitted by cormorants will amplify the effect of direct shark predation. Future studies will be needed, however, to confirm the potential indirect effects of tiger sharks on cormorant prey.

Tiger shark prey that use subsurface escape to avoid tiger sharks show markedly different microhabitat shifts in response to variation in tiger shark densities. Dolphins and dugongs distribute themselves across shallow seagrass banks approximately in proportion to the abundance of food when sharks are scarce (Heithaus & Dill 2006; Wirsing *et al.* 2007b). When shark density increases, dugongs, dolphins, and green turtles in good body condition concentrate along the edges of shallow banks where shark abundance also is highest despite greater foraging options available in interior microhabitats. This counterintuitive habitat shift likely arises because shallow edge microhabitats afford dugongs, dolphins, and green turtles greater escape success if they encounter a tiger shark compared to that in interior microhabitats where escape options are limited by water depth and distance to deep water where they can outmaneuver tiger sharks (Heithaus & Dill 2006; Heithaus *et al.* 2006, 2007; Wirsing *et al.* 2007b; Fig. 2). Thus, overall risk to these subsurface escaping species is lower in edge microhabitats despite higher predator encounter rates.

Our multiple-prey assessment of anti-predator behaviour in Shark Bay suggests not only that species manage overall risk rather than making habitat use decisions based on predator abundance alone, but that landscape attributes interact with specific anti-predator tactics to determine the sub-component of predation risk (i.e. encounter probability or conditional probability of prey death given encounter) that is weighed most heavily. In situations where these probabilities are both high in areas where predators are concentrated, or for species that select habitat primarily based on encounter rates (such as cormorants in Shark Bay), risk effects of predators should amplify those of direct predation and, thus, behaviourally mediated indirect species interactions and density-mediated indirect species interactions will work in concert. In contrast, when escape probability and predator abundance are negatively correlated, as they are for dolphins, dugongs and green turtles, the arrival of predators in an area can result, counter-intuitively, in increased mesoconsumer abundance in areas of high predator density and should result in increased exploitation rates. In the case of Shark Bay, dugongs and dolphins actually avoid more productive feeding areas that appear safer based on predator densities but where they are less likely to escape from a shark they encounter. Under these conditions, the indirect interaction between top predators and basal resources would be negative in a food chain with an odd number of trophic levels, while typical approaches to predator-prey interactions would incorrectly predict a positive indirect interaction. Although we do not have data on exploitation rates of teleosts by dolphins, patterns of seagrass nutrient composition in Shark Bay support the hypothesized reversal of indirect effects mediated by shifts in the distribution of dugongs. Seagrasses in edge microhabitats, where sharks are most abundant, have lower organic carbon content, which is indicative of elevated levels of grazing, relative to seagrasses in interior microhabitats (Heithaus *et al.* 2007).

Reversals in predicted indirect effects of top predators on basal resources mediated by landscape features may also occur in terrestrial systems. For example, Lima (1993) suggested that physical habitat structure and specific escape tactics of North American birds might interact to structure ecological interactions. Similarly, in and adjacent to Banff National Park, Canada, elk are found in higher densities in grasslands where wolf densities are the highest but escape probabilities are as well (Hebblewhite, Merrill & McDonald 2005). Similarly, in the northern range of Yellowstone National Park, USA, kill rates of elk are not related to wolf densities and are instead determined primarily by landscape features favourable to wolf hunting (Kauffman *et al.* 2007). In this system, social constraints on wolf habitat use and movements may be responsible for the decoupling of predation rates and predator densities (Kauffman *et al.* 2007). Similar decoupling of predator densities with those of particular prey species may occur when generalist predators have multiple possible prey types, which can reduce the likelihood that a predator will switch habitats in response to movements by single prey types (i.e. reduce game aspects of predator and

Fig. 3. Conceptual model for predicting risk effects, and resulting behaviourally mediated indirect effects, of predators in natural communities. Single-factor effects are indicated by black arrows. Two-way interactions are gray and the three-way interaction is represented by the dashed line and arrow. Specific dynamics of factors and interactions are given next to lines. This general framework underscores the degree to which natural history details are required to predict community dynamics. Also, it allows for the probability of being killed by a predator to be decomposed to varying degrees (e.g. to subdivide the conditional probability of prey death in an encounter situation into the probability of attack and probability of escape). Thus, anti-predator tactics (e.g. grouping, escape tactics, investment in vigilance) may interact with predator hunting mode to influence both the probability of attack in an encounter situation and the probability of escape given an attack. Both of these probabilities may further be influenced by physical features of the landscape ('landscape effects'; e.g. presence of cover).



prey habitat selection) (Heithaus 2001a). This appears to be the case for tiger sharks and their prey in Shark Bay. In such situations, a negative correlation between overall predation risk and predator density is possible and using predator abundance instead of assays of consumer behaviour to assess spatial variation in risk may lead to erroneous conclusions (Lima 1992; Brown & Kotler 2004; Kauffman *et al.* 2007). Thus, we suggest that the difficulty in developing a general framework for predicting community dynamics may in part be attributed to the need to account for the interaction of landscape variation and anti-predator behaviour in structuring the spatiotemporal patterns of mesoconsumer densities and exploitation of their resources.

Our study thus adds to the growing body of evidence suggesting that a predictive framework of community dynamics requires a basic understanding not only of the potential importance of nonconsumptive predator effects (e.g. Schmitz, Krivan & Ovadia 2004; Preisser *et al.* 2005; Schmitz 2006; Creel *et al.* 2007) but also of the basic natural history of predator and prey habitat use and predator- and habitat-dependent risk effects (Schmitz 2007). In particular, we suggest that the ability to predict community dynamics requires an understanding of predator hunting mode (which might also include the degree of territoriality, as in the wolf example of Kauffman *et al.* 2007), habitat-dependent anti-predator tactics of prey, and especially their interactions (Fig. 3). Landscape features will interact not only with anti-predator tactics, as we have shown here, but also with predator hunting mode and social structure (e.g. Kauffman *et al.* 2007; Preisser, Orrock & Schmitz 2007; Schmitz 2007). For example, in our case, even though tiger sharks are roving predators (Heithaus *et al.* 2002), they cause large spatial shifts in their prey because of the heterogeneous landscape (see Heithaus *et al.*

2008). Such risk effects of tiger sharks are akin to those predicted for sit-and-wait predators in a homogeneous landscape (Schmitz *et al.* 2004).

The framework we propose (e.g. Fig. 3) allows ecologists to further decompose the stages in a predator-prey interaction to make predictions about particular systems. In the Shark Bay system we have described, the assumptions that predator encounter rates are proportional to predator abundance and that the conditional probability of prey death is influenced largely by the interaction of escape tactics and landscape structure are appropriate. However, in other systems such assumptions may not hold. For example, African wild dog (*Lyncaon pictus*) encounter rates with prey vary based on the size of prey groups, prey type, and wild dog pack size (Creel & Creel 2002). Also, dogs are less likely to attack prey they are unlikely to catch. From the perspective of prey, then, dissuading attack may be as important as escape probability (Creel & Creel 2002). Differences between the Shark Bay and wild dog systems (i.e. in the latter, the need to decompose conditional probabilities of prey death in an encounter situation into attack and escape probabilities and the lack of concordance between encounter rates and predator density), however, are still captured by the main effects and interactions of predator hunting mode, prey anti-predator tactics, and landscape effects shown in Fig. 3.

Resolving the context dependence of predator risk effects on prey and resulting trait (including behaviour)-mediated indirect interactions is an important challenge in community ecology that will require closer attention to the natural history of predator-prey interactions. The similarity in anti-predator behaviour and risk effects among vastly different systems and species (Schmitz 2006; Heithaus *et al.* 2008) suggests that such an approach can lead to generalizable insights for predicting community dynamics.

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