



Cross-fertilizing aquatic and terrestrial research to understand predator risk effects

Aaron J. Wirsing,^{1,*†} Michael R. Heithaus^{2,†} and Alejandro Frid^{3,†}

Research that conceptually transcends boundaries between aquatic and terrestrial ecosystems has a long history of increasing insight into ecology and evolution. To stimulate further cross-fertilization between studies that focus on different ecosystems, we highlight several insights on risk effects—the costs of antipredator behavior—that have emerged in part because of combined advances in aquatic and terrestrial systems. Namely, risk effects (1) are not restricted to structured landscapes where antipredator behavior is easily measurable, (2) can be substantial even when prey experience very low predation rates, (3) are contingent on a three-way interaction between the hunting mode of the predator, escape tactic of the prey, and features of the landscape/physical environment, and (4) can interact with direct predation (consumption) and resource availability (through its effects on prey energy state) to control consumer population size. We conclude by highlighting the value of exploring differences between aquatic and terrestrial risk effects and offering a prospectus for future studies of antipredator behavior and its ecological importance in both eco-domains. © 2014 Wiley Periodicals, Inc.

How to cite this article:
WIREs Water 2014. doi: 10.1002/wat2.1039

G. C. Williams, originator of the theory of fish schooling that I am here supporting (Williams, 1964, 1966) points out that schooling is particularly evident in the fish that inhabit open waters. This fits with the view that schooling is similar to cover-seeking in its motivation. His experiments showed that fish species whose normal environment afforded cover in the form of weeds and rocks had generally less marked schooling tendencies. Among mammals, similarly, the most gregarious species are inhabitants of open grassy plains rather than of forest (Hesse, Allee & Schmidt, 1937). With fish schools observers have noted the apparent uneasiness of the outside fish and their eagerness for an opportunity to bury themselves in

the throng (Springer, 1957) and a parallel to this is commonly seen in the behaviour of the hindmost sheep that a sheepdog has driven into an enclosure: such sheep try to butt or to jump their way into the close packed ranks in front. Behaviour of this kind certainly cannot be regarded as showing an unselfish concern for the welfare of the whole group.

—W. D. Hamilton (1971)

INTRODUCTION

Cross-fertilization of research in freshwater, marine, and terrestrial ecosystems has a long history of increasing insight into ecology and evolution that goes back to at least Darwin and his contemporaries. Hamilton's¹ work on the geometry of the selfish herd provides a case in point. As illustrated by the 43-year-old quotation opening this essay, observations from both marine fish and ungulates inspired his ground-breaking insights on the antipredator benefits of group living. Moreover, cross-fertilization between aquatic and terrestrial eco-domains continues to advance modern ecology.^{2–4} For example, removal

*Correspondence to: wirsinga@uw.edu

¹School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA

²Department of Biological Sciences, Florida International University, North Miami, FL, USA

³Central Coast Indigenous Resource Alliance, Bowen Island, BC, Canada

[†]These authors contributed equally.

Conflict of interest: The authors have declared no conflicts of interest for this article.

experiments aimed at testing the effects of particular species on community interactions were employed first by marine and freshwater ecologists but now are applied widely to terrestrial food webs.^{5,6} The metabolic theory of ecology,⁷ which predicts organismal responses to environmental change, diffused in the opposite direction.⁸ Behavioral ecologists have also benefited greatly from cross-ecosystem comparisons. For instance, comparative studies between odontocete cetaceans and primates have yielded general insights into the function of coalitions and other social behaviors (e.g., Ref 9). Despite these examples, however, ecologists often underutilize the potential benefits of thinking outside the confines of a particular eco-domain.^{4,10–13}

Research into predator risk effects illustrates how removing conceptual boundaries across freshwater, marine, and terrestrial domains can strengthen ecological insights. Risk effects are the nonconsumptive effects of predators on prey, namely the lost foraging opportunities and lower levels of growth and reproduction experienced by prey investing in antipredator behavior. These effects are increasingly recognized for their potential to influence prey populations, community organization, and ecosystem dynamics.^{14–19} This growth of interest in risk effects owes much to cross-fertilization between laboratory and mesocosm studies in different ecosystems (e.g., Ref 20). Our experience is, however, that many ecologists studying large-bodied taxa (e.g., ungulates) under natural field conditions often are unaware of research on risk effects outside of their eco-domains. Such insular ecology arguably has limited understanding of the ecological role of large vertebrates in general and marine ones in particular.^{18,21–23} Here, we synthesize insights arising from cross-fertilization of aquatic and terrestrial studies on the ecological consequences of antipredator behavior, highlight the value of studying how risk effects might differ in these two environments, and provide a prospectus for future work.

THE SCOPE OF ANTIPREDATOR BEHAVIOR

There is a growing effort to elucidate the consequences of risk effects for community properties. This effort has primarily entailed the use of mesocosm experiments (e.g., see Ref 20 for a review) or fieldwork in aquatic and terrestrial systems where, from the researcher's perspective, well-defined landscape structures (i.e., patchiness) facilitate measures of variability in antipredator behavior (e.g., habitat shifts and use of refugia,²⁴ and giving-up densities¹⁵). Moreover, it has focused largely on invertebrate

or small-bodied herbivores that are amenable to experimentation²⁵ and that may experience high predation rates. In contrast, risk effects are less studied where spatial structure (patchiness) is less definable (e.g., pelagic marine systems^{26,27}) or where the prey assemblage is composed of large-bodied marine mesopredators or herbivores that, perhaps owing to high investment in antipredator behavior, can have low predation rates.²²

In patchy landscapes, which characterize many terrestrial ecosystems and littoral and benthic zones within aquatic ecosystems, it is well documented that prey individuals often respond to predation risk by shifting to safer habitats or by increasing vigilance. These responses carry the cost of lower foraging rates or reduced access to resources^{15,24} and, at least in risky patches, may also transmit positive indirect relationships between predators and species eaten by mesoconsumers [i.e., trait-mediated trophic cascades, which include behavior-mediated trophic cascades (BMTC)¹⁶]. Habitat shifts in response to predation risk are more difficult to document and often go unrecognized in pelagic habitats of the ocean and in limnetic and profundal zones of freshwater systems, which are less discrete, yet such shifts certainly occur. For example, one of the largest migrations of biomass on the planet—the downward movement of zooplankton to deep strata during daylight hours and then back to surface waters at night (diel vertical migration, DVM)—appears to be driven by risk from visually orienting fish predators that hunt near the surface during the day.^{28,29} Similar patterns of predator-induced DVM have been documented in freshwater planktivores.³⁰ Given the pervasiveness of DVM, does the paucity of evidence for open-water habitat shifts in response to predation risk reflect a lack of looking by researchers rather than the implausibility of these behaviors?²⁷ Answering this question will, in our view, be expedited by two developments. First, recognizing that open-water systems are, in fact, structured in a way that can facilitate spatial shifts (e.g., in terms of oceanic fronts and plankton patches³¹), should allow ecologists to become more aware that risk effects are plausible in these systems. Further—as illustrated by the quotation opening this essay—aquatic species in open water can also effectively create patchiness by schooling.¹ Large schools of fish, for instance, effectively represent patches offering heightened safety (e.g., via predator detection, confusion, and/or risk dilution) and within which danger can vary as a function of group position. This idea appears to apply in riverine ecosystems as well. For example, Orpwood et al.³² showed that European minnows (*Phoxinus phoxinus*) in seminatural stream

channels formed larger shoals in response to predation risk, but only in structurally simple habitats. Second, risk-induced shifts already are well documented in many systems where researchers can define landscape structure more easily. Awareness of that evidence should remove conceptual barriers for testing the plausibility of similar behaviors in the more subtle patchiness of open-water systems. For example, experiments in old-field meadows found that grasshoppers at risk of predation from spiders avoided the bottom strata of vegetation—where dangerous spiders and preferred food were most abundant—and increased use of the safer but food-poorer canopy.³³ These experiments inspired behavioral models for pinnipeds (i.e., large marine mesopredators) under risk of predation by deep-water sharks. Similar to the spider–grasshopper system, these models predicted that pinnipeds would optimize risk-energy trade-offs by avoiding more dangerous and food-richer deep strata and instead foraging more safely (at a feeding cost) in shallower strata^{34,35}; empirical data provided preliminary support for these predictions.³⁵ Similarly, Kramer³⁶ was inspired by the application of the marginal value theorem³⁷ to patch-leaving decisions by bees to develop one of the earliest models of the optimal dive cycle by air-breathing foragers (e.g., sea turtles, diving ducks, and marine mammals). Kramer's work, in turn, led to optimal dive cycle models that incorporated predation risk³⁸ based on the μ/g rule—a theory inspired by freshwater fishes which predicts that foragers minimize the ratio of predation risk experienced to unit of energy gained.³⁹

In the mid-1990s, there was little appreciation for the possibility that large-bodied marine herbivores (sea cows and sea turtles) and mesopredators (e.g., cetaceans and pinnipeds), which have low predation rates in many areas, respond to predation risk by shifting foraging habitats.²² At the time, our research on antipredator responses by large marine consumers in Shark Bay, Australia, was motivated instead by field research from the terrestrial realm documenting risk-induced behavioral adjustments by large-bodied species, including upper trophic-level predators (painted dogs, *Lycaon pictus*⁴⁰), herbivores (wildebeest, *Connochaetes taurinus*⁴¹), and primates (baboons, *Papio cynocephalus ursinus*⁴²). Using the ideal-free distribution framework, which was developed initially for understanding the use of reproductive resources by birds,⁴³ we have inferred how spatiotemporal variation in the risk of predation from tiger sharks (*Galeocerdo cuvier*) affects four long-lived marine mesopredators—Indian Ocean bottlenose dolphins (*Tursiops aduncus*⁴⁴), olive-headed sea snakes (*Distria major*⁴⁵), bar-bellied sea snakes

(*Hydrophis elegans*⁴⁶), and pied cormorants (*Phalacrocorax varius*²¹) (see Ref 47 for a review). All of these mesopredators trade food for safety by shifting into food-poor but safe habitats when threatened with shark predation. Large marine herbivores in this system also show marked risk sensitivity despite rarely succumbing to predation. For example, dugongs (*Dugong dugon*) in Shark Bay sacrifice food (seagrass) for safety by shifting from seagrass patches into deep water where seagrass is scarce,⁴⁸ avoiding the interior portions of seagrass meadows where access to safe deep water is reduced,⁴⁹ avoiding the use of a profitable foraging tactic—seagrass rhizome excavation—that constrains vigilance,⁵⁰ and by altering their dive cycles⁵¹ when confronted with tiger shark predation risk. Recent evidence from whales further challenges the idea that risk-induced spatial shifts, and other forms of antipredator behavior, are restricted to small-bodied aquatic species that suffer heavy predation rates. Specifically, Curé et al.⁵² found that sperm whales (*Physeter macrocephalus*) interrupt foraging dives and surface to form groups, thereby giving up food for safety, when exposed to sounds of mammal-feeding killer whales (*Orcinus orca*).

THE CONTINGENCY OF RISK EFFECTS

The threat of predation often induces behavioral modification (e.g., avoidance and increased vigilance) that reduces prey foraging investment.^{24,53} Consequently, predator presence is generally assumed to benefit species serving as food for prey. Growing evidence suggests, however, that this assumption may not always be valid and that prey responses to predators—and, therefore, the strength of risk effects—instead vary with context.^{19,21,23,54} For example, recent studies in a terrestrial old-field ecosystem show that grasshopper responses to spider predators depend on whether the spiders are active (roving) or sit-and-wait (ambush) hunters.²⁵ Ambush spiders leave persistent, point-source cues of predation risk, to which herbivorous grasshoppers can respond with chronic habitat shifts, whereas roving spiders do not leave such cues. Consequently, ambush spiders indirectly benefit nutritious grasses by inducing grasshoppers to shift their foraging activity to less preferred plant species, whereas roving spiders do not trigger habitat shifts. Instead, roving spiders have stronger consumptive effects on grasshoppers and thus differ in the kinds of indirect effects that they exert on plants.²⁵ A recent meta-analysis suggests that this dichotomy in prey responses based on predator hunting mode likely is widespread.⁵⁴

When applied to the Shark Bay ecosystem, these results might suggest that tiger sharks, which are roving predators, should elicit relatively little response in their prey. As we have already discussed, however, several prey species in this system manifest strong behavioral responses when in the presence of this roving predator. This disparity likely owes to the spatial predictability of tiger shark encounter rates in Shark Bay and the capacity of many of its prey species to reduce their probability of shark mortality through spatial shifts.²¹ That is, the grasshoppers studied by Schmitz and coworkers are found in a relatively homogeneous landscape where encounters with roving spiders are unpredictable. Conversely, tiger sharks in Shark Bay are found in a patchy landscape where they prefer shallow, seagrass-covered banks to deeper water.⁵⁵ Thus, some prey species (e.g., bottlenose dolphins and dugongs) avoid tiger sharks by spending less time in shallow habitats.^{44,48} Interestingly, tiger sharks also prefer peripheral (edges) to central (interiors) portions of seagrass meadows.⁵⁵ As a result, some prey species (e.g., olive-headed sea snakes) foraging over these meadows increase their use of interiors when confronted with tiger shark risk.^{21,45} Others (e.g., bottlenose dolphins and dugongs), however, actually spend more time foraging along seagrass meadow edges when threatened by sharks because their mode of escape (subsurface flight into deep water) confers the best overall probability of surviving a shark attack in this microhabitat despite lower predator encounter rates in interiors.^{49,56}

The combined insight of studies from aquatic and terrestrial domains and both small-scale experiments and large-scale observational studies suggests that predator risk effects and resulting indirect effects are influenced by a three-way interaction between the hunting mode of the predator, the escape tactic of the prey, and physical features of the landscape in which the encounter takes place.^{21,23} Consistent with the work on spider predators by Schmitz, prey responses are indeed contingent on predator hunting mode. Our marine studies suggest, however, that roving predators can nevertheless trigger antipredator behavior and risk effects on communities that cascade to primary producer communities and perhaps beyond⁵⁷ if landscape heterogeneity creates spatial variability in the effectiveness of prey escape responses. Although more work is needed to establish its generality across eco-domains, this framework is supported by studies in both aquatic and terrestrial systems. For example, roving adult perch (*Perca fluviatilis*) predators elicit divergent spatial shifts by juvenile perch (into open water) and roach (*Rutilus rutilus*) (into cover), presumably because different parts of the environment

offer an escape advantage for these two prey species.⁵⁸ Similarly, in stream pools, differential responses of herbivorous minnows (*Campostoma anomalum*) and crayfish (*Orconectes viridis*) to predatory largemouth bass (*Micropterus salmoides*) propagated variable indirect effects on algae.⁵⁹ Namely, antipredator responses by minnows, which shoal as a defense against bass, triggered whole-pool increases in algal height. In contrast, defensive responses by crayfish, which hide in burrows when threatened, led to increases in algal height that were concentrated along pool edges. Finally, on the Alberta prairie, Lingle⁶⁰ showed that roving coyotes (*Canis latrans*) trigger spatial shifts by mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) that are explained by prey escape behavior. Specifically, mule deer shift to broken terrain, where their escape tactics (active defense and bounding) are facilitated, whereas white-tailed deer shift to gentle terrain, where their sprinting escape tactic is most effective.

THE IMPORTANCE OF STATE-DEPENDENT RISK TAKING

According to state-dependent risk-taking theory, prey individuals experiencing resource shortages or low energy reserves should invest less in safety to avoid starvation or reduced reproductive potential and, therefore, suffer higher predation rates than conspecifics with greater energy stores.^{61,62} This idea took hold in terrestrial field studies relatively early on. For example, Sinclair and Arcese⁴¹ found that reductions in food supply on the African Serengeti appear to lead wildebeest (*C. taurinus*) to increase foraging risks and, as a result, succumb more frequently to lion (*Panthera leo*) predation. More recently, this framework has been applied and supported in large-scale aquatic ecosystems. For example, using whole-lake experiments, Biro et al.⁶³ showed that food addition led to decreased risk taking and—owing to lower predation rates—68% higher survival in age-0 rainbow trout (*Oncorhynchus mykiss*). Furthermore, inspired in part by Sinclair and Arcese⁴¹ and mesocosm experiments involving larval amphibians by Anholt and Werner,⁶⁴ theoretical simulations have predicted that a decline of near-surface fatty fish (e.g., herring *Clupea palassi*) in Prince William Sound, and therefore reduced energy stores, would induce Steller sea lions (*Eumetopias jubatus*) and harbor seals (*Phoca vitulina*) to increase their risk taking by making more deep foraging dives, thereby incurring higher predation rates inflicted by deep-dwelling Pacific sleeper sharks (*Somniosus pacificus*).^{35,65} Their findings also prompted research in Shark Bay showing that green turtles (*Chelonia*

mydas) in poor condition spend a large proportion of their foraging time over the interior portions of shallow seagrass meadows, where they can access high-quality seagrass but are subject to a heightened risk of mortality from tiger sharks.⁶⁶ Conversely, green turtles in good physical condition, which make up most of the local population, forage primarily along the periphery of seagrass meadows where escape from tiger sharks into deep water is facilitated. By implication, much of Shark Bay's seagrass is little used by green turtles because tiger sharks render it too dangerous to exploit, and therefore both food and predation by sharks control the number of green turtles in the ecosystem.

The general insight that emerges from integrating research on state-dependent risk taking in different eco-domains is twofold. First, resource declines or chronic resource limitation (i.e., bottom-up forces) could reduce levels of antipredator investment within populations of large consumers by depressing average condition and, as a result, indirectly increase direct predation rates (i.e., top-down forces) experienced by these populations.^{18,35,41,61,64,65} Recently, for example, a long-term decline in food supply has been invoked to explain increased risk taking and predation mortality in the marine bivalve (*Macoma balthica*).⁶⁷ Interestingly, this same scenario (termed the 'Stalingrad' effect)⁶⁸ could be unfolding in the Greater Yellowstone Ecosystem, where a recent study during a period of prolonged drought and nutrient limitation found only modest evidence for costly antipredator investment in elk (*Cervus elaphus*) relative to earlier investigations.⁶⁹ More broadly, among herbivores at least, terrestrial species are more likely to be nutrient limited and require high-quality forage than their aquatic counterparts.⁷⁰ Consequently, under this state-dependent risk-taking model, herbivores in terrestrial systems may be forced into riskier foraging decisions, and thereby suffer higher predation rates, than those in aquatic environments. If, on the other hand, levels of antipredator investment remain stable despite long-term resource declines, then large consumer populations could be depressed through declines in state-dependent reproductive rates (e.g., Ref 71). Thus, in both aquatic and terrestrial systems, a dichotomous 'top-down versus bottom-up' approach that invokes either direct predation or resource quality as the sole driver of consumer densities and community properties may be flawed. Second, because of the dynamic interplay between consumer condition, risk taking, and vulnerability to predation, predators are more likely to affect consumer populations predominantly through the interaction between risk and consumptive effects, rather than by

consumptive effects or risk effects alone^{18,47} (see also Refs 14 and 16). For example, predators can depress prey populations solely via prey starvation stemming from antipredator investment or via the combination of risk-induced starvation and increased predation on risk-prone individuals in compromised condition.⁴⁷

DIFFERENCES BETWEEN AQUATIC AND TERRESTRIAL RISK EFFECTS

Another potential benefit of cross-fertilization is the opportunity to identify fundamental differences between freshwater aquatic, marine, and terrestrial realms that might lead to divergent risk effects or variation in their relative importance in population and community dynamics. A recent cross-system comparison of predator-prey body-mass ratios, for example, suggests that size constraints on trophic interactions are weaker in terrestrial than in aquatic systems. In an aquatic medium that lacks hard surfaces, prey not swallowed whole are likely to sink or be swept away and lost.⁷² By implication, size constraints on the nonconsumptive effects of gape-limited aquatic predators may be more pronounced than those on terrestrial predators. Furthermore, some top aquatic predators are highly mobile and migrate seasonally while their prey species remain within the same area year-round (e.g., tiger sharks in Shark Bay⁷³). As a result, nonmigratory aquatic prey species may experience 'risk-released' conditions for greater periods of time than their counterparts in terrestrial systems, where top predators are often more closely tied to localized patterns of prey abundance (e.g., gray wolves⁷⁴). Terrestrial systems with seasonally migrating avian predators, on the other hand, could serve as an interesting basis for comparison of the effects of periodic risk release in aquatic and terrestrial environments. Many aquatic predators, including sharks, exhibit indeterminate growth and ontogenetic dietary shifts. Accordingly, a research approach that transcends ecosystem boundaries would help to determine whether metrics such as body size and trophic level might be more informative than terrestrial-derived ways of categorizing the risk effects, and ecological roles, of predators (i.e., apex- and mesopredation).⁷⁵ Finally, open-water systems are by nature three dimensional and usually lack complete refuges, thus requiring antipredator behaviors that differ from those in structured coastal marine (e.g., coral or rocky reefs), freshwater, and terrestrial environments where complete refugia are available. Antipredator behavior that may apply to open-water systems (e.g., group formations or movement patterns that confuse predators or dilute risk²⁶), in turn, may offer insights into

the kinds of antipredator behavior we might expect to observe in benthic, littoral, and terrestrial systems where habitat structure is poorly defined.

BOX 1

THE INFLUENCE OF VISIBILITY ON RISK EFFECTS IN AQUATIC AND TERRESTRIAL ECOSYSTEMS

Recent work in terrestrial ecosystems has opened a debate on the importance of predator risk effects in structuring ecosystems. Namely, in Yellowstone National Park, early studies suggested that a BMTC, whereby the presence of wolves (*Canis lupus*) induces habitat shifts and changes in foraging behavior of elk (*Cervus elaphus*) that release riparian vegetation from herbivory, was critical to structuring the ecosystem.⁷⁶ More recently, this view has been challenged.^{77,78} Winnie⁷⁸ suggested that under current conditions a BMTC might not occur because elk are able to detect the presence or absence of wolves in a general region and take advantage of low-risk periods to forage in habitats that would be too dangerous if wolves were present. This scenario raises the question of whether the strong risk effects of tiger sharks in Shark Bay⁴⁷ are facilitated by the poor underwater visibility that characterizes the area.⁵⁷ That is, unlike in Yellowstone, Shark Bay's turbidity may prevent potential prey, which rely primarily on vision to detect sharks, from tracking the presence of their predators and responding to risk at fine spatiotemporal scales. Rather, limited visibility in this ecosystem may necessitate more dramatic trade-offs based on general encounter and escape probabilities (e.g., avoidance of large areas where escape is inhibited when tiger sharks are present in the ecosystem). In accord with this idea, a recent terrestrial review⁷⁹ found that, for nocturnal prey species that orient visually, low visibility enhanced the effect of predation risk on foraging (activity correlated positively with moonlight), presumably because these species are best able to detect and avoid predators under well-lit conditions. Similarly, Iribarren and Kotler⁸⁰ found that Nubian ibex (*Capra nubiana*) displayed greater investment in antipredator vigilance when in the presence of sight-line obstructions. By implication, an understanding of factors that modify visibility should help to explain the nature and strength of risk effects in both aquatic and terrestrial ecosystems. Furthermore, absorption and scattering of light are more pronounced in aquatic environments,⁸¹

limiting the range of visual interactions relative to that in terrestrial ecosystems.⁸² Thus, when light is available, terrestrial prey species may generally be better able to perceive and respond to predation risk at fine spatiotemporal scales than those in aquatic ecosystems.

CONCLUSION

Cross-fertilization of research in terrestrial, freshwater, and marine ecosystems has long enhanced our understanding of antipredator behavior and its ecological consequences. Hamilton's¹ seminal work (our opening example) recognized that the antipredator benefits of shoaling by fish in open-water habitats are analogous to those of group formation by social species in open, terrestrial environments. Hamilton's selfish herd hypothesis continues to inform our understanding of animal group formation. For example, predatory attacks by free-ranging white sharks (*Carcharodon carcharias*) on Cape fur seal (*Arctocephalus pusillus*) decoys (i.e., simulated prey) matched Hamilton's prediction that tighter interindividual distances reduce predation risk for individual members of a group.⁸³ Many studies of risk effects and other ecological phenomena, however, have underutilized the potential benefits of thinking beyond the confines of their focal eco-domain.^{4,12,13}

We have highlighted general insights into the risk effects of predators that have emerged, at least in part, from cross-system comparison, arguing for broader conceptual exchange across the land–water divide. Our review suggests that aquatic ecology (and especially research in systems lacking well-defined habitat structure) can benefit from a greater appreciation of (1) the general importance of risk effects, (2) the potential influence of predator hunting mode on antipredator behavior, and (3) the expectation that mesopredators, not unlike herbivores, also respond behaviorally to predation risk. Terrestrial ecologists, on the other hand, would benefit from the idea that prey with different escape tactics could respond differently to the same predator and even show opposite patterns of spatial shifts.^{21,23} Furthermore, researchers from both realms will gain from insight into the factors that could differentiate risk effects in the water and on land, including visibility (Box 1). Therefore, synergy between marine and terrestrial ecologists should yield a broader framework for understanding and predicting the effects of predation risk on prey behavior and the dynamics of communities and ecosystems.

ACKNOWLEDGEMENTS

We thank C. Torgersen for providing the initiative for this work and are grateful to B. Kotler and an anonymous referee for providing helpful feedback. This paper was funded in part by National Science Foundation grants (DEB1145902) to AJW, (OCE0526065, OCE0745606, and DBI0620409) to MRH, and an NSERC IRDF fellowship to AF. This paper is contribution number 75 of the Shark Bay Ecosystem Research Project.

REFERENCES

1. Hamilton WD. Geometry for the selfish herd. *J Theor Biol* 1971, 31:295–311. doi: 10.1016/0022-5193(71)90189-5.
2. Cole JJ. Communication between terrestrial and marine ecologists: loud, sometimes abrasive, but healthy and occasionally useful. *Mar Ecol Prog Ser* 2005, 304: 272–274.
3. Stenseth NC, Mysterud A, Durant JM, Hjermann DO, Ottersen G. Uniting ecologists into a smooth, tasty and potent blend. *Mar Ecol Prog Ser* 2005, 304:289–292.
4. Menge BA, Chan F, Dudas S, Eerkes-Medrano D, Grorud-Colvert K, Heiman K, Hessing-Lewis M, Lles A, Milston-Clements R, Noble M, et al. Do terrestrial ecologists ignore aquatic literature? *Front Ecol Environ* 2009, 7:182–183. doi: 10.1890/09.WB.010.
5. Paine RT. Food webs – linkage, interaction strength, and community infrastructure – the 3rd Tansley Lecture. *J Anim Ecol* 1980, 49:667–685.
6. Raffaelli D, Solan M, Webb TJ. Do marine and terrestrial ecologists do it differently? Bridging the gap between aquatic and terrestrial ecology. *Mar Ecol Prog Ser* 2005, 304:283–289.
7. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. Toward a metabolic theory of ecology. *Ecology* 2004, 85:1771–1789. doi: 10.1890/03-9000.
8. Duarte CM. Marine ecology warms up to theory. *Trends Ecol Evol* 2007, 22:331–333. doi: 10.1016/j.tree.2007.04.001.
9. Connor RC. Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philos Trans R Soc B: Biol Sci* 2007, 362:587–602. doi: 10.1098/rstb.2006.1997.
10. Steele JH. Can ecological theory cross the land-sea boundary? *J Theor Biol* 1991, 153:425–436. doi: 10.1016/S0022-5193(05)80579-X.
11. Chase JM. Are there real differences between aquatic and terrestrial food webs? *Trends Ecol Evol* 2000, 15:408–412. doi: 10.1016/S0169-5347(00)01942-X.
12. Webb TJ. Marine and terrestrial ecology: unifying concepts, revealing differences. *Trends Ecol Evol* 2012, 27:535–541. doi: 10.1016/j.tree.2012.06.002.
13. Rotjan RD, Ijdadi J. Surf and turf: toward a better synthesis by cross-system understanding. *Oikos* 2013, 122:285–287. doi: 10.1111/j.1600-0706.2013.21047.x.
14. Werner E, Peacor S. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 2003, 84:1083–1100. doi: 10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2.
15. Brown JS, Kotler BP. Hazardous duty pay and the foraging cost of predation. *Ecol Lett* 2004, 7:999–1014. doi: 10.1111/j.1461-0248.2004.00661.x.
16. Schmitz OJ, Krivan V, Ovadia O. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol Lett* 2004, 7:153–163. doi: 10.1111/j.1461-0248.2003.00560.x.
17. Creel S, Christianson D. Relationships between direct predation and risk effects. *Trends Ecol Evol* 2008, 23:194–201. doi: 10.1016/j.tree.2007.12.004.
18. Heithaus MR, Frid A, Wirsing AJ, Worm B. Predicting ecological consequences of marine top predator declines. *Trends Ecol Evol* 2008, 23:202–210. doi: 10.1016/j.tree.2008.01.003.
19. Schmitz OJ. Effects of predator hunting mode on grassland ecosystem function. *Science* 2008, 319:952–954. doi: 10.1126/science.1152355.
20. Preisser EL, Bolnick DL, Benard MF. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 2005, 86:501–509. doi: 10.1890/04-0719.
21. Heithaus MR, Wirsing AJ, Burkholder D, Thomson J, Dill LM. Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *J Anim Ecol* 2009, 78:556–562. doi: 10.1111/j.1365-2656.2008.01512.x.
22. Wirsing AJ, Heithaus MR, Frid A, Dill LM. Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals. *Mar Mamm Sci* 2008, 2:1–15. doi: 10.1111/j.1748-7692.2007.00167.x.
23. Wirsing AJ, Cameron KE, Heithaus MR. Spatial responses to predators vary with prey escape mode. *Anim Behav* 2010, 79:531–537. doi: 10.1016/j.anbehav.2009.12.014.

24. Lima SL, Dill LM. Behavioural decisions made under the risk of predation: a review and prospectus. *Can J Zool* 1990, 68:619–640.
25. Schmitz OJ. Predators avoiding predation. *Proc Natl Acad Sci U S A* 2008, 105:14749–14750. doi: 10.1073/pnas.0808033105.
26. Dill LM, Heithaus MR, Walters CJ. Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology* 2003, 84:1151–1157. doi: 10.1890/0012-9658(2003)084[1151:BMIIIM]2.0.CO;2.
27. Heithaus MR, Wirsing AJ, Frid A, Dill LM. Behavioral indicators in marine conservation: lessons from a pristine seagrass ecosystem. *Isr J Ecol Evol* 2007a, 53:355–370. doi: 10.1560/IJEE.53.3.355.
28. Lampert W. The adaptive significance of diel vertical migration of zooplankton. *Funct Ecol* 1989, 3:21–27 Available at: <http://links.jstor.org/sici?doi=0269-8463%281989%293%3A1%3C21%3ATASODV%3E2.0.CO%3B2-Y>.
29. Hays GC. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 2003, 503:163–170. doi: 10.1023/B:HYDR.0000008476.23617.b0.
30. Gjelland KO, Bohn T, Horne JK, Jensvoll I, Knudsen FR, Amundsen P. Planktivore vertical migration and shoaling under a subarctic light regime. *Can J Fish Aquat Sci* 2009, 66:525–539. doi: 10.1139/F09-014.
31. Wedding LM, Leoczyk CA, Pittman SJ, Friedlander AM, Jorgensen S. Quantifying landscape structure: extending terrestrial spatial pattern metrics to the marine realm. *Mar Ecol Prog Ser* 2011, 427:219–232. doi: 10.3354/meps09119.
32. Orpwood JE, Magurran AE, Armstrong JD, Griffiths SW. Minnows and the selfish herd: effects of predation risk on shoaling behavior are dependent on habitat complexity. *Anim Behav* 2008, 76:146–152. doi: 10.1016/j.anbehav.2008.01.016.
33. Schmitz OJ. Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol Lett* 2003, 6:156–163. doi: 10.1046/j.1461-0248.2003.00412.x.
34. Frid A, Baker GG, Dill LM. Do shark declines create fear-released systems? *Oikos* 2008, 117:191–201. doi: 10.1111/j.2007.0030-1299.16134.x.
35. Frid A, Burns J, Baker GG, Thorne RE. Predicting synergistic effects of resources and predators on foraging decisions by juvenile Steller sea lions. *Oecologia* 2009, 158:775–786. doi: 10.1007/s00442-008-1189-5.
36. Kramer DL. The behavioral ecology of air breathing by aquatic animals. *Can J Zool* 1988, 66:89–94. doi: 10.1139/z88-012.
37. Charnov EL. Optimal foraging, the marginal value theorem. *Theor Popul Biol* 1976, 9:129–136. doi: 10.1016/0040-5809(76)90040-X.
38. Heithaus MR, Frid A. Optimal diving under the risk of predation. *J Theor Biol* 2003, 223:79–92. doi: 10.1016/S0022-5193(03)00073-0.
39. Gilliam JF, Fraser DF. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 1987, 68:1856–1862. doi: 10.2307/1939877.
40. Mills MGL, Gorman ML. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conserv Biol* 1997, 11:1397–1406 Available at: <http://www.jstor.org/stable/2387366>.
41. Sinclair ARE, Arcese P. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology* 1995, 76:882–891. doi: 10.2307/1939353.
42. Cowlishaw G. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim Behav* 1997, 53:667–686. doi: 10.1006/anbe.1996.0298.
43. Fretwell SD, Lucas HL. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor* 1969, 19:16–36. doi: 10.1007/BF01601953.
44. Heithaus MR, Dill LM. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 2002, 83:480–491. doi: 10.2307/2680029.
45. Wirsing AJ, Heithaus MR. Olive-headed sea snakes *Distinctia major* shift seagrass microhabitats to avoid shark predation. *Mar Ecol Prog Ser* 2009, 387:287–293. doi: 10.3354/meps08127.
46. Kerford MR, Wirsing AJ, Heithaus MR, Dill LM. Danger on the rise: diurnal tidal state mediates an exchange of food for safety by the bar-bellied sea snake *Hydrophis elegans*. *Mar Ecol Prog Ser* 2008, 358:289–294. doi: 10.3354/meps07346.
47. Heithaus MR, Wirsing AJ, Dill LM. The ecological importance of intact top predator populations: a synthesis of 15 years of research in a seagrass ecosystem. *Mar Freshw Res* 2012, 63:1039–1050. doi: 10.1071/MF12024.
48. Wirsing AJ, Heithaus MR, Dill LM. Fear factor: do dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)? *Oecologia* 2007, 153:1031–1040. doi: 10.1007/s00442-007-0802-3.
49. Wirsing AJ, Heithaus MR, Dill LM. Living on the edge: dugongs prefer to forage in microhabitats allowing for escape from rather avoidance of predators. *Anim Behav* 2007, 74:93–101. doi: 10.1016/j.anbehav.2006.11.016.
50. Wirsing AJ, Heithaus MR, Dill LM. Can you dig it? Use of excavation, a risky foraging tactic, by dugongs is sensitive to predation danger. *Anim Behav* 2007, 74:1085–1091. doi: 10.1016/j.anbehav.2007.02.009.
51. Wirsing AJ, Heithaus MR, Dill LM. Predator-induced modifications to diving behavior vary with foraging mode. *Oikos* 2011, 120:1005–1012. doi: 10.1111/j.1600-0706.2010.18844.x.

52. Curé C, Antunes R, Alves AC, Visser F, Kvadsheim PH, Miller PJO. Responses of male sperm whales (*Physeter macrocephalus*) to killer whale sounds: implications for anti-predator strategies. *Sci Rep* 2013, 3:1579. doi: 10.1038/srep01579.
53. Werner EE, Hall DJ. Ontogenetic shifts in bluegill: the foraging rate–predation risk trade off. *Ecology* 1988, 69:1352–1366. doi: 10.2307/1941633.
54. Preisser EL, Orrock JL, Schmitz OJ. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology* 2007, 88:2744–2751. doi: 10.1890/07-0260.1.
55. Heithaus MR, Hamilton IM, Wirsing AJ, Dill LM. Validation of a randomization procedure to assess animal habitat preferences: microhabitat use of tiger sharks in a seagrass ecosystem. *J Anim Ecol* 2006, 75:666–676. doi: 10.1111/j.1365-2656.2006.01087.x.
56. Heithaus MR, Dill LM. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos* 2006, 114:257–264. doi: 10.1111/j.2006.0030-1299.14443.x.
57. Burkholder DA, Heithaus MR, Fourqurean JW, Wirsing A, Dill LM. Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade? *J Anim Ecol* 2013, 82:1192–1202. doi: 10.1111/1365-2656.12097.
58. Eklöv P, Persson L. The response of prey to the risk of predation: proximate cues for refuging juvenile fish. *Anim Behav* 1996, 51:105–115. doi: 10.1006/anbe.1996.0009.
59. Gelwick FR. Grazer identity changes the spatial distribution of cascading trophic effects in stream pools. *Oecologia* 2000, 125:573–583.
60. Lingle S. Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology* 2002, 83:2037–2048. doi: 10.1890/0012-9658(2002)083[2037:CPAHSO]2.0.CO;2.
61. McNamara JM, Houston AI. Starvation and predation as factors limiting population size. *Ecology* 1987, 68:1515–1519. doi: 10.2307/1939235.
62. Clark CW. Antipredator behaviour and the asset-protection principle. *Behav Ecol* 1994, 5:159–170. doi: 10.1093/beheco/5.2.159.
63. Biro PA, Post JR, Parkinson EA. From individuals to populations: prey fish risk-taking mediates mortality in whole-system experiments. *Ecology* 2003, 84:2419–2431. doi: 10.1890/02-0416.
64. Anholt BR, Werner EE. Interactions between food availability and predation mortality mediated by adaptive behavior. *Ecology* 1995, 76:2230–2234. doi: 10.2307/1941696.
65. Frid A, Baker GG, Dill LM. Do resource declines increase predation rates on North Pacific harbor seals? *Mar Ecol Prog Ser* 2006, 312:265–275. doi: 10.3354/meps312265.
66. Heithaus MR, Frid A, Wirsing AJ, Dill LM, Fourqurean JW, Burkholder D, Thomson J, Bejder L. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *J Anim Ecol* 2007, 76:837–844. doi: 10.1111/j.1365-2656.2007.01260.x.
67. Van Gils JA, Kraan C, Dekkinga A, Koolhaas A, Drent J, de Goeij P, Piersma T. Reversed optimality and predictive ecology: burrowing depth forecasts population change in a bivalve. *Biol Lett* 2009, 5:5–8. doi: 10.1098/rsbl.2008.0452.
68. Brown JS, Kotler BP, Mitchell WA. Competition between birds and mammals: a comparison of giving-up densities between larks and gerbils. *Evol Ecol* 1997, 11:757–771. doi: 10.1023/A:1018442503955.
69. Middleton AD, Kauffman MJ, McWhirter DE, Jimenez MD, Cook RC, Cook JG, Albeke SE, Sawyer H, White PJ. Linking anti-predator behavior to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecol Lett* 2012, 16:1023–1030. doi: 10.1111/ele.12133.
70. Burkepile DE. Comparing aquatic and terrestrial grazing ecosystems: is the grass really greener? *Oikos* 2013, 122:306–312. doi: 10.1111/j.1600-0706.2012.20716.x.
71. Creel S, Winnie JA Jr, Christianson D. Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. *Proc Natl Acad Sci U S A* 2009, 106:12388–12393. doi: 10.1073/pnas.0902235106.
72. Brose U, Jonsson T, Berlow EL, Warren P, Banasek-Richter C, Bersier L, Blanchard JL, Brey T, Carpenter SR, Blandenier MC, et al. Consumer-resource body-size relationships in natural food webs. *Ecology* 2006, 87:2411–2417. doi: 10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2.
73. Wirsing AJ, Heithaus MR, Dill LM. Tiger shark (*Galeocerdo cuvier*) abundance and growth in a subtropical embayment: evidence from 7 years of standardized fishing effort. *Mar Biol* 2006, 149:961–968. doi: 10.1007/s00227-006-0278-4.
74. Jedrzejewski W, Schmidt K, Theuerkauf J, Jedrzejewski B, Okarma H. Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Białowieża Primeval Forest in Poland. *Can J Zool* 2001, 79:1993–2004. doi: 10.1139/cjz-79-11-1993.
75. Huepel MR, Knip DM, Simpfendorfer CA, Dulvy NK. Sizing up the ecological role of sharks as predators. *Mar Ecol Prog Ser* 2014, 495:291–298. doi: 10.3354/meps10597.
76. Ripple WJ, Beschta RL. Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience* 2004, 54:755–766. doi: 10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2.
77. Kauffman MJ, Brodie JF, Jules ES. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally-mediated trophic cascade. *Ecology* 2010, 91:2742–2755. doi: 10.1890/09-1949.1.

78. Winnie JA Jr. Predation risk, elk, and aspen: tests of a behaviorally mediated trophic cascade in the Greater Yellowstone Ecosystem. *Ecology* 2012, 93:2600–2614. doi: 10.1890/11-1990.1.
79. Prugh LR, Golden CD. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *J Anim Ecol* 2014, 83:504–514. doi: 10.1111/1365-2656.12148.
80. Iribarren C, Kotler BR. Patch use and vigilance behaviour by Nubian ibex: the role of the effectiveness of vigilance. *Evol Ecol Res* 2012, 14:223–234.
81. Lythgoe JN. Light and vision in the aquatic environment. In: Atema J, Fay RR, Popper AN, Tavoga N, eds. *Sensory Biology of Aquatic Animals*. New York: Springer-Verlag; 1988, 57–82 doi:10.1007/978-1-4612-3714-3_3.
82. Hansen AG, Beauchamp DA, Baldwin CM. Environmental constraints on piscivory: insights from linking ultrasonic telemetry to a visual foraging model for cutthroat trout. *Trans Am Fish Soc* 2013, 142:300–316. doi: 10.1080/00028487.2012.732650.
83. De Vos A, O'Riain MJ. Sharks shape the geometry of a selfish seal herd: experimental evidence from seal decoys. *Biol Lett* 2010, 6:48–50. doi: 10.1098/rsbl.2009.0628.