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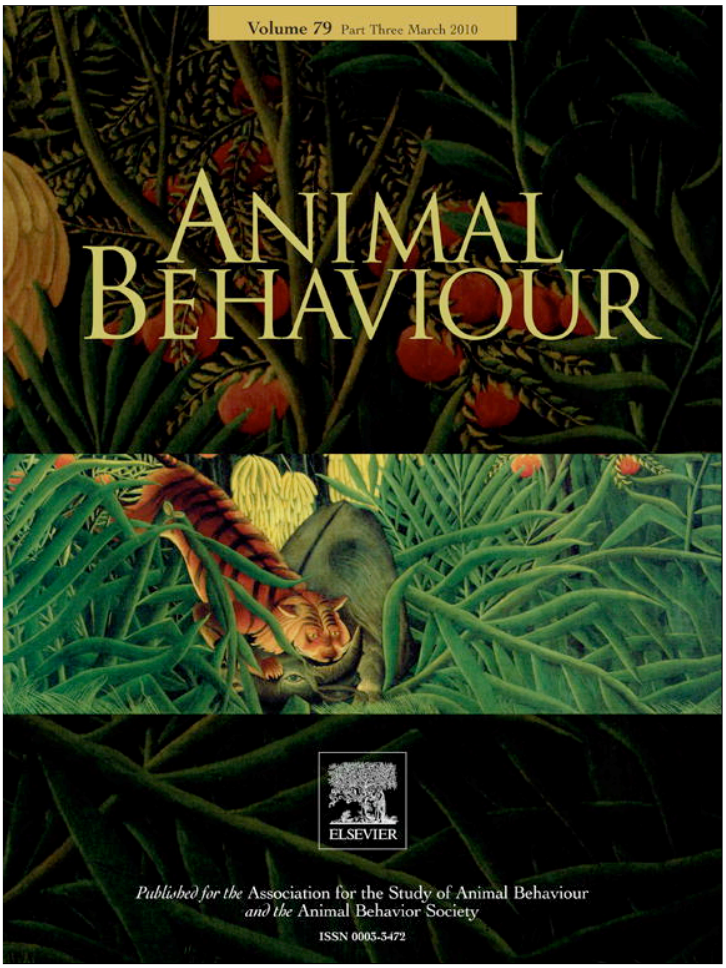

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Review

Spatial responses to predators vary with prey escape mode

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Prey often avoid their predators but may, under certain conditions, remain in or even shift to space where predators are relatively abundant when threatened. Here, we review studies of habitat choices by multiple, sympatric prey species at risk from a shared predator to show that the defensive decision to avoid or select predator-rich space is contingent on prey escape behaviour. We suggest that prey species with escape tactics offering little chance of survival following an encounter should seek predator scarcity, whereas those with tactics whose post-encounter effectiveness is spatially correlated with predator abundance should be most likely to match the distribution of their predators. Furthermore, we argue that the nature of the defensive spatial response of a prey species with a particular escape tactic also depends on the hunting approach used by its predator and the setting of the predator–prey interaction (i.e. landscape features). Accordingly, an integrated approach that accounts for prey escape behaviour and the context provided by predator hunting mode and landscape features should lead to a better understanding of antipredator spatial shifts and improve our ability to anticipate the consequences of changes in predator numbers for prey distributions and ecosystem dynamics. We conclude by encouraging further exploration of contingency in antipredator behaviour and the possibility that generalist predators might indirectly influence prey resources and community properties via diverse pathways that are mediated by spatial shifts of prey species with different escape tactics.
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The propensity for predators to influence prey demography and trophic interactions via induced behaviour is now widely appreciated (Lima 1998; Preisser et al. 2005; Creel & Christianson 2008; Heithaus et al. 2008). Behavioural responses to predators often manifest as habitat shifts (Brown & Kotler 2004), which can redistribute spatial patterns of resource exploitation by prey, modify competitive interactions, and help to organize communities (Werner & Peacor 2003; Schmitz et al. 2004). Prey are typically assumed to avoid their predators (Lima 1998), leading to the widespread expectation that these spatial shifts should produce community changes consistent with reduced prey foraging and competition where predators are abundant and increased prey foraging and competition where predators are relatively scarce. An emerging view holds, instead, that prey behavioural responses to predators depend upon system-specific features of the interaction in question and, as a result, the consequences of antipredator habitat shifts will not always follow this pattern (Preisser et al. 2007; Schmitz 2007, 2008; Heithaus et al. 2009). By implication, efforts to identify the factors that determine how individuals use space when threatened with predation are crucial to the development of a general framework for predicting the effects of predators on their prey and ecosystems.

Lima (1992) introduced the idea that escape behaviour could lead to contingency in the responses of prey to predation risk. Given that any prey individual's overall risk of predation can be decomposed into its probability of encountering a predator (pre-encounter risk) and its probability of death as a result of the encounter (post-encounter risk) (Lima & Dill 1990; Hugie & Dill 1994), Lima demonstrated theoretically that, to improve their overall fitness, prey species with certain escape tactics might actually select space where predators are relatively abundant but less lethal. Conversely, prey species lacking the ability to increase their chances of escape sufficiently via spatial shifts would be expected to reduce encounters by seeking relatively predator-free space. A logical extension of this demonstration is that predators could exert diverse and sometimes spatially opposing indirect effects on prey resources and community properties mediated by spatial shifts of prey species with different means of escape. Although few would probably argue with the premise that complexity of adaptive decision making by prey could lead species with particular traits to eschew predator avoidance, Lima's idea has received surprisingly little attention. Indeed, most studies continue to neglect crucial details of prey escape behaviour that may help decide outcomes of predator–prey interactions (Heithaus et al.

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2009). Enough empirical work finally exists, however, to allow for broad exploration of the degree to which variation in escape behaviour leads sympatric prey species with shared predators to make different habitat choices in response to risk.

Here, we review and synthesize these studies to illustrate (1) the strong link between variation in escape behaviour and differential habitat choice by sympatric prey under threat of predation and (2) the consistency with which this link is maintained across taxa and across aquatic, marine and terrestrial systems. We also discuss how escape behaviour variation might interact with other key factors upon which antipredator responses are contingent (predator hunting mode, landscape features) to govern defensive space use decisions by prey. Finally, we identify pathways for future research on these factors that should facilitate explanation and prediction of antipredator space use behaviour.

DEFINING ESCAPE BEHAVIOUR

We defined escape behaviour as any behaviour that improves a prey individual's likelihood of survival once it encounters (i.e. detects the presence of) a predator. Thus, escape behaviours could include those allowing for early predator detection once a prey individual is within the predator's perceptual range (i.e. enabling prey to win the detection game) and various forms of active defence, fleeing (i.e. evasion) and hiding (using cover, crypsis, or inactivity/freezing).

LINKING ESCAPE BEHAVIOUR AND HABITAT CHOICE: EMPIRICAL EXAMPLES

We based our review on 17 studies documenting variable space use decisions in response to risk from a shared predator (or predators) by multiple, sympatric prey species that were attributable to interspecific differences in escape behaviour (Table 1). We restricted our survey to peer-reviewed studies with nonanecdotal results that are not confounded by alternative interpretations based on interspecific competition and/or spatiotemporal variation in food resources. We also did not include studies in systems where spatial segregation of predator species hindered differentiation of habitat shifts reducing predator encounters from those promoting escape and where all focal prey species did not share the same predator or predators.

Aquatic Systems

In aquatic systems, predator hunting success is often inversely proportional to habitat complexity (e.g. cover availability, degree of structure), leading many prey species in these systems to select complex habitats when threatened with predation (Gotceitas & Colgan 1989). Yet, selection for habitat complexity in aquatic systems appears to be contingent on prey escape behaviour. For example, Savino & Stein (1989) found that two sympatric lacustrine fishes with different escape tactics, the bluegill, *Lepomis macrochirus*, and the fathead minnow, *Pimephales promelas*, made contrasting choices between high- and low-cover habitat following exposure to predation risk from largemouth bass, *Micropterus salmoides*, and northern pike, *Esox lucius*. Specifically, bluegills, which escape predators by seeking obstructive cover (Moody et al. 1983), shifted into cover-rich habitat even though both predators showed a preference for these habitats. Conversely, minnows, which escape predation by dispersing into open water, reduced their use of cover-rich areas, thereby avoiding their predators.

Two lacustrine studies of space use by juvenile perch, *Perca fluviatilis*, and roach, *Rutilus rutilus*, threatened by piscivorous adult perch reveal divergent shifts with respect to habitat complexity that are attributable to escape behaviour. A comparison of the two studies also indicates that preference for any type of complexity by prey individuals can depend on the degree to which it facilitates their means of escape. Eklöv & Persson (1996) found that juvenile perch, which are slow swimmers and escape predation by hiding, shifted away from cover-rich (artificially vegetated) habitat occupied by adult perch and into predator-free open habitat. In contrast, roach, which are fast swimmers that escape predators by fleeing and leaping out of the water, moved into high-cover habitat once risk was introduced despite the absence of adult perch in the open. By implication, without viable hiding options in either habitat, juvenile perch shifted spatially to facilitate avoidance, while selection of space replete with both cover and predators by roach can best be explained as a means of enhancing their probability of escape. When confronted with a different choice between open habitat near the water's surface and bottom crevices (complex habitat) following exposure to risk, roach selected open water, while juvenile perch sought hiding cover provided by bottom crevices (Christensen & Persson 2005). Predator density in this latter study was spatially consistent, so the two prey species appear to have made contrasting habitat choices that facilitated their respective modes of escape. Interestingly, roach chose habitat complexity in one case and eschewed it in the other, suggesting that the nature (artificial vegetation versus bottom crevices), rather than mere presence, of complexity is a driver of defensive space use by some aquatic species.

Peckarsky (1996) found that four stream-dwelling invertebrates (the mayfly species *Baetis bicaudatus*, *Cinygmula* sp., *Epeorus longimanus*, *Ephemerella infrequens*) with different escape tactics displayed varying degrees of risk-induced avoidance of foraging substrate following exposure to predatory stoneflies (*Megarcys signata*). Specifically, *B. bicaudatus*, which swims or drifts in the water column when threatened by predators, abandoned foraging substrate and suffered a reduced resource acquisition rate following exposure to *M. signata*. In contrast, two heptageniid mayflies (*Cinygmula* sp., *E. longimanus*) with a crawling escape response showed a weaker tendency to avoid *M. signata* and sacrificed less food in response to predator presence. Finally, *E. infrequens*, which freezes when under threat of predation, did not avoid *M. signata* and, presumably, experienced minimal loss in foraging efficiency.

Marine Systems

Ryer et al. (2004) showed that two benthic flatfishes, juvenile Pacific halibut, *Hippoglossus stenolepis*, and juvenile northern rock sole, *Lepidopsetta polyxystra*, with different escape modes displayed varying degrees of preference for sediment with emergent structure (sponges) over substrates with bare, sandy substrates following exposure to age-2 halibut predators. Specifically, juvenile halibut, which escape by flushing, preferred sediments with sponges because they reduce the capture efficiency of age-2 halibut during chases even though these habitats were relatively predator-rich. Conversely, juvenile rock sole, which escape using crypsis, showed no preference for either habitat.

In the coastal sea grass ecosystem of Shark Bay, Australia, four large vertebrates (Indian Ocean bottlenose dolphins, *Tursiops aduncus*, dugongs, *Dugong dugon*, olive-headed sea snakes, *Disteria major*, and pied cormorants, *Phalacrocorax varius*) make contrasting shifts between interior (central) and edge (peripheral) microhabitats over shallow sea grass banks when faced with the threat of tiger shark, *Galeocerdo cuvier*, predation. When tiger sharks are present, bottlenose dolphins and dugongs, which escape predators by fleeing into and outmanoeuvring their attackers in deeper water, shift to the edge of sea grass banks where shark abundance is relatively high (Heithaus et al. 2006), but escape probability is greater due to access to deeper waters (Heithaus & Dill 2006;

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Table 1
Summary of studies demonstrating antipredator behavioural responses that are contingent upon prey escape mode. Prey species in bold are those that, as a defensive response, actually remain in or shift into predator-rich habitats or microhabitats (i.e. do not avoid their predators)

Study system	Predator(s)	Prey	Contingent behaviour(s)	Reference(s)
Aquatic				
Lacustrine	Largemouth bass, *Micropterus salmoides* Northern pike, *Esox lucius*	**Bluegill, *Lepomis macrochirus*** Fathead minnow, *Pimephales promelas*	Use of open and cover-rich habitats	Savino & Stein 1989
Lacustrine	Adult perch, *Perca fluviatilis*	Juvenile perch, *P. fluviatilis* **Roach, *Rutilus rutilus***	Use of habitats with and without vegetative cover	Eklöv & Persson 1996
Lacustrine	Adult perch, *Perca fluviatilis*	Juvenile perch, *P. fluviatilis* Roach, *Rutilus rutilus*	Use of habitats with and without bottom structure (crevices)	Christensen & Persson 2005
Lotic	Stonefly, *Megarcys signata*	Mayflies (*Baetis bicaudatus*, *Cinygmula* sp., *Epeorus longimanus*, *Ephemerella infrequens*)	Tendency to abandon foraging substrate	Peckarsky 1996
Marine				
Benthic	Age-2 halibut, *Hippoglossus stenolepis*	**Age-0 halibut, *H. stenolepis*** Rock sole, *Lepidopsetta polyxystra*	Use of two benthic habitats offering different amounts of structure	Ryer et al. 2004
Coastal sea grass ecosystem	Tiger shark, *Galeocerdo cuvier*	**Bottlenose dolphin (*Tursiops* sp.)** **Dugong, *Dugong dugon*** Olive-headed sea snake, *Disteria major* Pied cormorant, *Phalacrocorax varius*	Use of two shallow sea grass bank microhabitats	Heithaus & Dill 2006; Wirsing et al. 2007; Wirsing & Heithaus 2009; Heithaus et al. 2009
Terrestrial				
Rocky outcrops	Human-simulated	Lizards (*Agama planiceps*, *Mabuya laevis*, *M. striata*, *M. sulcata*, *M. variegate*, *Rhotropus boultoni*)	Use of rocky microhabitats prior to entry into a refuge	Cooper & Whiting 2007
Old agricultural field	Northern harrier, *Circus cyaneus*	Savannah sparrow, *Passerculus sandwichensis* Song sparrow, *Melospiza melodia*	Use of habitats with high and low ground cover	Watts 1990
Old agricultural field	Raptors	Lark bunting, *Calamospiza melanocorys* White-crowned sparrow, *Zonotrichia leucophrys*	Foraging location in relation to cover	Lima 1990
Open, semi-desert grassland	Primarily prairie falcon, *Falco mexicanus*	Chipping sparrow, *Spizella passerina* Vesper sparrow, *Pooecetes gramineus* Savannah sparrow, *P. sandwichensis* *Ammodramus* sparrows Meadowlarks (*Sturnella* spp.)	Use of open patches following addition of woody cover	Lima & Valone 1991
Spruce-fir forest	Domestic ferret, *Mustela furo*	Horned lark, *Eremophila alpestris* *Deer mouse, Peromyscus maniculatus* Red-backed vole, *Clethrionomys gapperi*	Use of habitats with variable amounts of cover	Wywialowski 1987
Prairie	Coyote, *Canis latrans*	**White-tailed deer, *Odocoileus virginianus*** Mule deer, *Odocoileus hemionus*	Use of sloped and gentle terrain	Lingle 2002
Mixed-forest	Wolf, *Canis lupus*	**Elk, *Cervus elaphus*** Moose, *Alces alces* **White-tailed deer, *Odocoileus virginianus***	Use of winter habitats	Kittle et al. 2008
Savanna	Lion, *Panthera leo*	Giraffe, *Giraffa camelopardalis* **Steinbuck, *Raphicerus campestris***	Use of complex (wooded) habitat	Riginos & Grace 2008

Wirsing et al. 2007). Conversely, olive-headed sea snakes and pied cormorants, which escape predators by hiding amidst bottom vegetation and taking to the air, respectively, choose interior microhabitats where the probability of encountering tiger sharks is relatively low (Wirsing & Heithaus 2009; Heithaus et al. 2009). The authors conclude that, when threatened, bottlenose dolphins and dugongs respond by making spatial adjustments that promote escape rather than avoidance, whereas olive-headed sea snakes and pied cormorants favour avoidance because their modes of escape are equally effective in both microhabitats (Wirsing & Heithaus 2009; Heithaus et al. 2009).

Terrestrial Systems

In a study set amongst rocky outcrops in northwestern Namibia, Cooper & Whiting (2007) found that six sympatric lizards with different escape tactics (*Agama planiceps*, *Mabuya laevis*, *M. striata*, *M. sulcata*, *M. variegate*, *Rhotropus boultoni*) made contrasting microhabitat choices when approached by a human-simulated predator. All six species use rock crevices as a refuge from predators, but their divergent means of escape into crevices apparently lead them to select different rocky microhabitats when threatened. *Agama planiceps* escapes into crevices by squirreling around boulders and therefore shifts to the top or far side of rocks after detecting danger. In contrast, *M. laevis*, *M. striata*, *M. sulcata* and *M. variegata* escape into crevices using direct sprints and, consequently, do not switch microhabitats until actually chased into a refuge by a predator. Finally, *Rhotropus boultoni* uses vertical surfaces and crypsis to facilitate escape into crevices and, as a result, seeks rocky microhabitat featuring steep sides and heavy shadows once it detects a predator. Divergent, predator-induced microhabitat shifts by these

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lizards prior to refuge entry could give rise to different foraging patterns.

Working in an old agricultural field system, Watts (1990) showed that two sparrows (song sparrow, *Melospiza melodia*, and Savannah sparrow, *Passerculus sandwichensis*) manifested different patterns of habitat selection while under threat of predation by the northern harrier, *Circus cyaneus*, that were explained by disparity between their escape tactics. Namely, reduction of ground cover via mowing induced avoidance by song sparrows, which use a cover-dependent escape tactic, but not by Savannah sparrows, which use an escape tactic (flight up to a perch) that is independent of cover availability. The shift by song sparrows away from mowed sites was clearly defensive given that they were far less likely to fall prey to harriers on cover-rich sites. Savannah sparrows were approximately 60 times less likely to fall prey to harriers than song sparrows in the absence of cover, suggesting that the effectiveness of their escape tactic in the open allowed them to continue using mowed sites. In another old field experiment, Lima (1990) found that two finches under threat of predation by raptors showed opposite patterns of space use in relation to cover while foraging that were explained by differences in escape behaviour. White-crowned sparrows, *Zonotrichia leucophrys*, which seek cover when attacked, preferred to feed in cover and never fed in its absence. Conversely, lark buntings, *Calamospizam elanocorys*, which do not seek cover when attacked and instead rely on aerial manoeuvres, avoided feeding in cover and fed in its absence. In an open, semi-desert grassland system, Lima & Valone (1991) showed that six avian species at risk of predation primarily by prairie falcons, *Falco mexicanus*, responded to habitat manipulation (cover addition) in a manner that was predicted well by the varying amounts of cover dependency in their escape behaviour. Species most dependent on cover for escape (i.e. that flush to cover when threatened; vesper sparrows, *Pooecetes gramineus*; chipping sparrows, *Spizella passerina*) increased their use of manipulated sites, while those whose escape mode was least dependent on cover (i.e. with aerial escape tactics) significantly decreased their use of (*Ammodramus* sparrows) or stopped using (horned lark, *Eremophila alpestris*) sites with added cover.

Wywialowski (1987) found that two rodents with different escape tactics (red-backed voles, *Clethrionomys gapperi*, and deer mice, *Peromyscus maniculatus*) manifested contrasting space use behaviour when exposed to predation risk from domestic ferrets, *Mustela furo*. Red-backed voles, which rely on quick manoeuvres around obstructions to evade predators, showed a strong preference for experimental chambers with high-cover density. In contrast, deer mice, which rely on raw speed to escape and have less need for obstructions, used both high- and low-cover chambers.

Predation risk from coyotes, *Canis latrans*, induces divergent habitat shifts by two prairie ungulates (white-tailed deer, *Odocoileus virginianus*, and mule deer, *Odocoileus hemionus*) that are driven by differences in prey escape behaviour (Lingle 2002). Following the approach of coyotes, white-tailed deer, which flee to escape predation, shifted down and away from slopes and on to gentle terrain where exposure to coyotes is elevated but their likelihood of surviving attacks is high. Conversely, mule deer, which actively defend against predation, shifted on to and up slopes, where food is scarce but their likelihood of encountering coyotes is relatively low. Mule deer mortality following encounters with coyotes was higher on gentle than on sloped terrain, while no such disparity existed for white-tailed deer. Thus, the efficacy of the white-tailed deer's escape tactic on flat ground apparently allows it to continue foraging on gentle terrain in the presence of coyotes, whereas the ineffectiveness of the mule deer's tactic forces it to exchange food for predator avoidance on steep slopes (Lingle 2002).

In a mixed deciduous–conifer forest system, three ungulates with different escape modes show variable patterns of defensive habitat use during winter while under risk of wolf, *Canis lupus*, predation (Kittle et al. 2008). White-tailed deer, which flee predators and rely on early detection, select open habitats with low snowfall and avoid areas with dense cover where their means of escape are inhibited (Kunkel & Pletscher 2001). Elk, *Cervus elaphus*, which also escape wolves by fleeing but are less reliant on early detection and use cover to facilitate evasion, selected sparse forest offering ample escape routes and vegetative cover while fleeing (Geist 1982). Interestingly, neither ungulate avoided wolves, instead choosing habitats where the likelihood of predator encounter was relatively high, implicating escape likelihood as the factor underlying their spatial shifts. In contrast, moose, *Alces alces*, did not select any particular habitat in response to wolves, probably because the efficacy of their escape mode, active defence, is high and less dependent on habitat features.

On the African savanna, Riginos & Grace (2008) found that two large herbivores (steinbuck, *Raphicerus campestris*, and giraffe, *Giraffa camelopardalis*) respond to the threat of lion, *Panthera leo*, predation with different space use decisions that are explained by their escape tactics. In this system, lions prefer to hunt in complex habitats where they are cryptic (Hopcraft et al. 2005). Accordingly, in response to lion predation risk, giraffes sacrifice rich food resources in these complex habitats for the safety of open areas, where they are both less likely to encounter lions and more likely to escape by fleeing. Steinbucks escape lion predation by freezing and sinking into ground vegetation. This cryptic escape tactic presumably is more successful where vegetation is dense than the fleeing tactic used by giraffes, allowing steinbuck to harvest the resources offered by complex habitats despite the danger posed by lions.

INTERACTION BETWEEN ESCAPE BEHAVIOUR AND OTHER DRIVERS OF ANTIPREDATOR HABITAT USE

Two external components of the predator–prey interaction have garnered attention as drivers of contingency in antipredator behaviour: predator hunting mode and landscape features. Both components probably interact with the escape tactic of any given prey species to help determine its spatial response to predation risk.

Predator Hunting Mode and Escape Behaviour

Antipredator decisions by prey can hinge on the hunting mode used by their predator (Sih et al. 1998). For example, Trinidadian guppies, *Poecilia reticulata*, respond to visually orienting pike cichlids, *Crenicichla frenata*, by spending more time near the water's surface, but they do not manifest this spatial shift when at risk from freshwater prawns, *Macrobrachium carcinus*, which hunt using olfactory cues (Botham et al. 2008). Consequently, sympatric predators can sometimes exert contrasting top–down effects on community properties through the same consumer. Schmitz (2008) showed, for instance, that differences in foraging by the herbivorous grasshopper *Melanopuls femurrubrum* while under threat from two spiders with different hunting modes gave rise to divergent grassland plant communities in mesocosms. Specifically, risk from the sit-and-wait predator *Pisaurina mira* induced *M. femurrubrum* to shift into refuge habitat where it feeds on the dominant herb *Solidago rugosa* and thereby led to increased plant diversity. Conversely, under risk from the actively hunting predator *Phidippus rimator*, *M. femurrubrum* did not manifest a spatial shift and, instead, fed on the competitively inferior grass *Poa pratensis*, leading to a less diverse plant community.

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Less attention has been devoted to the additional possibility that, in multiprey systems with shared predators, interaction between predator hunting mode and escape behaviour could help to determine whether prey species with different escape tactics show contrasting habitat shifts. That is, predator hunting approaches that are equally effective against all prey escape modes in a habitat would be expected to promote similar antipredator shifts among prey species irrespective of escape behaviour (e.g. uniformly away from the habitat if it is where the predator is most effective). Furthermore, hunting approaches that are equally effective across all escape modes and habitats should uniformly promote predator avoidance. Conversely, hunting modes that differ in efficacy across space in a manner that varies with escape behaviour would be expected to promote variability in antipredator space use, with each prey species selecting the habitat in which its escape tactic is most effective against the predator. For example, while Eklöv & Persson (1996) found that actively hunting adult perch elicit divergent habitat shifts by juvenile perch (into open habitat) and roach (into cover), they also discovered that ambushing pike evoke the same habitat shift in these species (selection for cover). We can surmise that both prey fishes gain an escape advantage against the hunting tactic used by pike in cover, promoting a similar shift into predator-rich space, whereas only roach gain an advantage against the hunting approach of adult perch in cover, leading to avoidance of this habitat type by juvenile perch.

Landscape Features and Escape Behaviour

The lethality of predators at any location is often influenced by attributes of the surrounding landscape (Gripenberg & Roslin 2007; Kauffman et al. 2007). Therefore, use of any habitat patch (or the direction of microhabitat shifts within a patch) by prey following exposure to predation danger can depend on the size, shape and composition of the patch relative to neighbouring patches. For example, Bowers & Dooley (1993) found that relative use of edge and interior feeding microhabitats within patches across an experimental landscape by white-footed mice, *Peromyscus leucopus*, and meadow voles, *Microtus pennsylvanicus*, following exposure to predation risk varied with patch size. Both species avoided edges, where predator hunting activity was concentrated, during risky intervals (full moon) when using large patches, but they did not manifest this apparently defensive microhabitat preference when using medium-sized patches. By implication, the relatively high interior-to-edge ratio characterizing medium-sized patches constrained the value of interior microhabitat as a refuge from predation.

In systems where generalist predators target multiple consumers, interaction between landscape features and prey escape behaviour can dictate the occurrence of contrasting patterns of defensive space use. For example, as described previously, white-crowned sparrows (*Z. leucophrys*, cover-dependent escape tactic) under predation risk fed in cover, whereas lark buntings (*C. elanocorys*, cover-independent escape tactic) fed in the open when feeding patches either featured or lacked cover (Lima 1990). When landscape configuration was altered such that feeding patches were never in cover but varied in their distance to cover, however, both species showed similar patterns of space use while foraging. By inference, the two species experienced differential escape efficiency across space under the former configuration, with the survival advantage gained by white-crowned sparrows in cover leading them to select cover-rich feeding sites and vice versa. This spatial disparity in escape efficiency apparently disappeared under the latter arrangement. In general, we suggest that landscapes allowing sympatric prey with divergent escape tactics to improve their chances of survival after a predator encounter by choosing different patch types are likely to promote contrasting antipredator spatial shifts and the possibility of counterintuitive selection for predator-rich space by at least some prey species. Conversely, landscapes that provide for enhanced effectiveness of all escape tactics in one patch type should promote similarity among spatial responses to risk, and those resulting in equal effectiveness of all escape modes across space should promote avoidance of patches where predators are abundant.

CONCLUSIONS AND FUTURE DIRECTIONS

We found multiple studies showing that prey escape behaviour gives rise to diverse spatial responses to predation risk and, in some counterintuitive cases, leads particular prey species to select space where predators are relatively common even in the absence of foraging rewards in these areas. Collectively, these studies invalidate the common assumption that overall predation risk is always highest where predators are most abundant and suggest that reliance on this assumption could lead to spurious conclusions about the reasons behind prey habitat choices. For example, if studies documenting selection of predator-rich areas by prey do not recognize the possibility that this pattern of space use may be a defensive response, they could lead to the erroneous conclusion that particular prey species are not influenced by predation risk and instead are either responding to food availability or showing maladaptive behaviour.

Our review also reveals disparities in the degree to which escape behaviour has been linked to variability in antipredator spatial shifts across systems and taxa. We found few studies documenting such a link in marine systems and using invertebrates. The paucity of studies correlating differential habitat use with escape diversity in marine systems is not surprising, given that escape tactics are difficult to ascertain in these systems and, perhaps more saliently, attention given to behavioural predator–prey interactions in marine communities has lagged behind that in aquatic and terrestrial domains (Dill et al. 2003). The dearth of examples involving invertebrates is harder to explain because their antipredator decisions are relatively easy to explore under experimental conditions, but it could derive from the general perception that invertebrates are behaviourally simple.

We also discovered surprising similarity in the way that species-specific habitat shifts by sympatric prey with divergent means of escape can lay the groundwork for predators in different ecosystem types to indirectly influence prey resources (e.g. producers like plants) via multiple pathways. For example, a series of marine studies (Heithaus & Dill 2006; Wirsing et al. 2007; Heithaus et al. 2009; Wirsing & Heithaus 2009) and a terrestrial study (Lingle 2002) showed that the presence of a predator (tiger sharks and coyotes, respectively) can drive certain prey species away while actually enhancing the density of others that are able to counteract high predator encounter rates with effective escape tactics (Fig. 1). In both systems, predators should indirectly benefit the resources of the prey species they repel and exert a negative indirect effect on resources of prey species they attract. Interestingly, patterns of sea grass chemical composition in Shark Bay are consistent with this expectation: inorganic and organic carbon concentrations indicate heavy grazing by dugongs along the periphery of sea grass banks relative to interiors (Heithaus et al. 2009), suggesting that, because the dugong's mode of escape leads it to match the distribution of its predator, tiger sharks indirectly benefit sea grass by providing a reprieve from herbivory where they are least numerous. More generally, the sign of the indirect interaction between predators and resources of their prey may be case specific and not always positive as is normally assumed.

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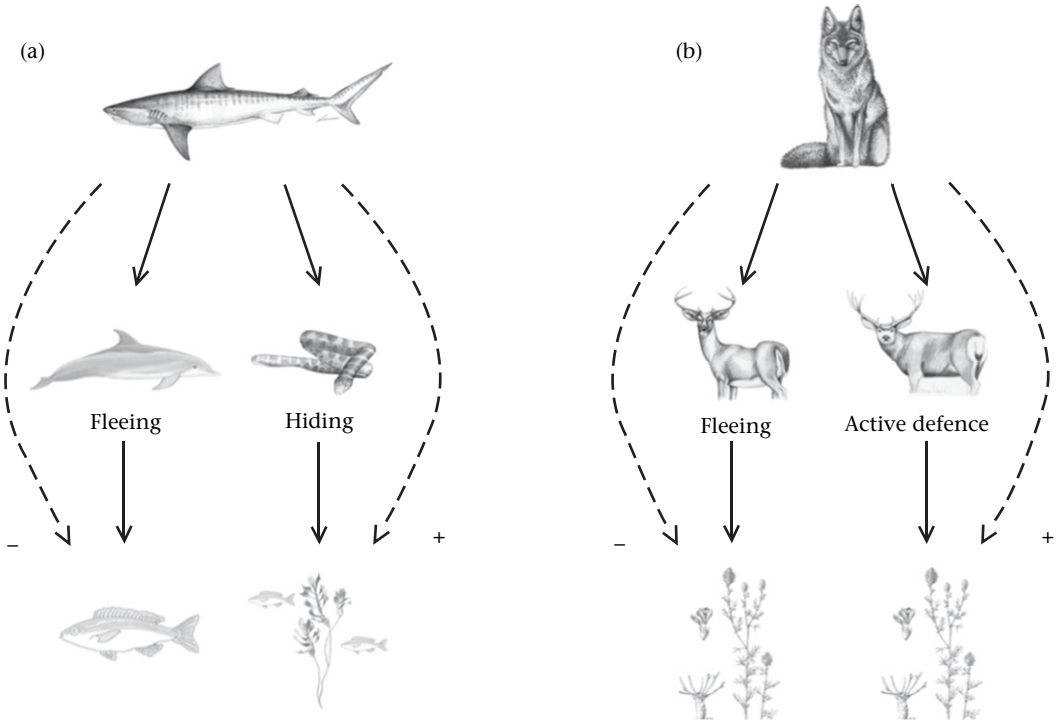

Figure 1. Contrasting hypothesized indirect effects of predators on prey resources (dashed arrows) transmitted by divergent behavioural responses of prey with differing escape tactics in a coastal marine and a terrestrial prairie ecosystem. (a) Along the periphery of shallow sea grass banks, tiger sharks, *Galeocerdo cuvier*, may exert a negative indirect effect on large sea grass fishes (e.g. western butterfish, *Pentapodus vita*; pictured) by attracting bottlenose dolphins (*Tursiops* sp.), which escape by fleeing into deeper habitat, and a positive indirect effect on small sea grass fishes (pictured with the sea grass *Amphibolis antarctica*) by repelling olive-headed sea snakes, *Disteria major*, which escape by hiding in bottom vegetation. (b) On gentle prairie terrain, coyotes, *Canis latrans*, could exert a negative indirect effect on grasses and forbs (e.g. purple prairie clover, *Petalostemum purpureum*; pictured) by attracting white-tailed deer, *Odocoileus virginianus*, which escape by fleeing, and a positive indirect effect on these plant species by repelling mule deer, *Odocoileus hemionus*, which escape using active defence. Note that solid arrows signify documented direct interactions.

How do we predict when prey at risk will make the counterintuitive decision to select space where predators are relatively abundant? For any prey species, we suggest that the answer to this question lies primarily in the prey's ability to improve its overall chances of survival by using predator-rich space. Accordingly, we would expect threat-sensitive prey species with great scope for reducing their post-encounter mortality risk by selecting areas where predators are abundant to be more likely to match the distribution of their predators, and species that do not enjoy markedly reduced vulnerability in predator-rich space to be more likely to show strong avoidance of predators. As we have argued, a species' scope for adjusting its likelihood of survival (post-encounter) via spatial shifts is largely determined by interactions between its escape mode and (1) the hunting tactic of the predator to which it is responding and (2) landscape features. That is, a prey species will be a good candidate for counterintuitive antipredator habitat use if the landscape allows for substantially heightened effectiveness of its mode of escape against the hunting approach of its predator in space where predators are relatively dense. Poor candidates will be species with escape tactics whose efficacy is either rendered spatially inflexible by characteristics of its predator and/or the landscape or greatest where predators are scarce. Importantly, under this framework, prey species with multiple escape modes may be good or poor candidates depending on the tactic they use when faced with a particular predator and landscape.

We caution that studies of contingency in antipredator space use must account for the possibility that similarity between predator and prey distribution attributed to escape behaviour is not instead the product of the predator's behaviour, interference from another predator, or social and nutritional constraints on prey individuals. Predators are active participants in predator–prey interactions and can respond to prey movements with spatial shifts (Lima 2002). Thus, matching predator and prey distributions (and diverse antipredator space use decisions by multiple prey species) could derive from active selection for space where a particular prey species is abundant by predators seeking high encounter rates (e.g. by specialists). In contrast, spatial matching that stems from shifts by prey species can best be identified when the habitat preference of the predator is fixed. Fixed predator distributions tend to occur when the habitat domain of the predator is limited (Schmitz 2007), an inverse spatial relationship between prey food availability and post-encounter risk leads predators to consistently select for areas where food for their prey is plentiful (Hugie & Dill 1994), and/or alternative prey are available (i.e. the predator is a generalist; Heithaus 2001). Prey are often subject to risk from multiple predators (Sih et al. 1998). Consequently, observed shifts into habitats where a focal predator is common by a prey species could represent an avoidance response to a second, more lethal predator that is rare or ignored. Finally, depressed nutritional condition and social constraints can provide little scope for antipredator investment (Heithaus et al. 2008) and, if widespread, lead to matches between predator and prey distribution.

The number of studies identifying drivers of contingency in antipredator behaviour is growing, but few demonstrate empirically that contrasting behavioural responses to shared predators by sympatric prey precipitate alternative indirect effects that cascade through communities. The types of experimental manipulations that can discriminate between indirect effects transmitted by prey with specific escape tactics are logistically problematic, so the paucity of such demonstrations is hardly surprising, but they have been undertaken (e.g. Schmitz 2008). Finally, therefore, we

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advocate exploration of the nature and importance of divergent indirect predator effects that are transmitted by contrasting spatial responses of sympatric prey. For example, there is need for studies addressing the magnitude, duration and spatial extent of alternate prey responses required to trigger divergent indirect effects. The implications of escape-driven contingency in antipredator habitat selection for competitive interactions between prey species also merit consideration, as does the capacity of bottom–up forces (i.e. resources) to promote or inhibit the existence of divergent indirect effects through their influence on prey risk taking. Studies of this kind will enhance our understanding of predator effects in communities and improve our ability to predict the consequences of predator removal and restoration for prey behaviour, the spatial patterns of foraging pressure experienced by prey resources, and the dynamics of ecosystems.

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References

Botham, M. S., Hayward, R. K., Morrell, L. J., Croft, D. P., Ward, J. R., Ramnarine, I. & Krause, J. 2008. Risk-sensitive antipredator behavior in the Trinidadian guppy, *Poecilia reticulate*. *Ecology*, **89**, 3174–3185.

Bowers, M. A. & Dooley, J. L. Jr. 1993. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. *Oecologia*, **94**, 247–254.

Brown, J. S. & Kotler, B. P. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, **7**, 999–1014.

Christensen, B. & Persson, L. 2005. Species-specific anti-predator behaviours: effects on prey choice in different habitats. *Behavioral Ecology and Sociobiology*, **32**, 1–9.

Cooper, W. E. & Whiting, M. J. 2007. Universal optimization of flight initiation distance and habitat-driven variation in escape tactics in a Namibian lizard assemblage. *Ethology*, **113**, 661–672.

Creel, S. & Christianson, D. 2008. Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, **23**, 194–201.

Dill, L. M., Heithaus, M. R. & Walters, C. J. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology*, **84**, 1151–1157.

Eklöv, P. & Persson, L. 1996. The response of prey to the risk of predation: proximate cues for refuging juvenile fish. *Animal Behaviour*, **51**, 105–115.

Geist, V. 1982. Adaptive behavioural strategies. In: *Elk of North America: Ecology and Management* (Ed. by J. W. Thomas & D. E. Toweill), pp. 219–278. Harrisburg, Pennsylvania: Stackpole.

Gotceitas, V. & Colgan, P. 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. *Oecologia*, **80**, 158–166.

Gripenberg, S. & Roslin, T. 2007. Up or down in space? Uniting the top–down versus bottom–up paradigm and spatial ecology. *Oikos*, **116**, 181–188.

Heithaus, M. R. 2001. Habitat selection by predators and prey in communities with asymmetrical intraguild predation. *Oikos*, **92**, 542–554.

Heithaus, M. R. & Dill, L. M. 2006. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos*, **114**, 257–264.

Heithaus, M. R., Hamilton, I. M., Wirsing, A. J. & Dill, L. M. 2006. Validation of a randomization procedure to assess animal habitat preferences: microhabitat use of tiger sharks in a seagrass ecosystem. *Journal of Animal Ecology*, **75**, 666–676.

Heithaus, M. R., Frid, A., Wirsing, A. J. & Worm, B. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, **23**, 202–210.

Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J. & Dill, L. M. 2009. Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *Journal of Animal Ecology*, **78**, 556–562.

Hopcraft, J. G., Sinclair, A. R. E. & Packer, C. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, **74**, 559–566.

Hugie, D. M. & Dill, L. M. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology, Supplement A*, **45**, 151–169.

Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R. & Boyce, M. S. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letters*, **10**, 690–700.

Kittle, A. M., Fryxell, J. M., Desy, G. E. & Hamr, J. 2008. The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia*, **157**, 163–175.

Kunkel, K. E. & Pletscher, D. H. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. *Journal of Wildlife Management*, **65**, 520–530.

Lima, S. L. 1990. Protective cover and the use of space: different strategies in finches. *Oikos*, **58**, 151–158.

Lima, S. L. 1992. Strong preferences for apparently dangerous habitats? A consequence of differential escape from predators. *Oikos*, **64**, 597–600.

Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, **27**, 215–290.

Lima, S. L. 2002. Putting predators back into behavioral predator–prey interactions. *Trends in Ecology & Evolution*, **17**, 70–75.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

Lima, S. L. & Valone, T. J. 1991. Predators and avian community organization: an experiment in a semi-desert grassland. *Oecologia*, **86**, 105–112.

Lingle, S. 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology*, **83**, 2037–2048.

Moody, R. C., Helland, J. M. & Stein, R. A. 1983. Escape tactics used by bluegills and fathead minnows to avoid predation by tiger muskellunge. *Environmental Biology of Fishes*, **8**, 61–65.

Peckarsky, B. L. 1996. Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. *Ecology*, **77**, 1888–1905.

Preisser, E. L., Bolnick, D. I. & Benard, M. F. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, **86**, 501–509.

Preisser, E. L., Orrock, J. L. & Schmitz, O. J. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology*, **88**, 2744–2751.

Riginos, C. & Grace, J. B. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom–up vs. top–down effects. *Ecology*, **89**, 2228–2238.

Ryer, C. H., Stoner, A. W. & Titgen, R. H. 2004. Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. *Marine Ecology Progress Series*, **268**, 231–243.

Savino, J. F. & Stein, R. A. 1989. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Environmental Biology of Fishes*, **24**, 287–293.

Schmitz, O. J. 2007. Predator diversity and trophic interactions. *Ecology*, **88**, 2415–2426.

Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science*, **319**, 952–954.

Schmitz, O. J., Krivan, V. & Ovadia, O. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, **7**, 153–163.

Sih, A., Enlund, G. & Wooster, D. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution*, **13**, 350–355.

Watts, B. D. 1990. Cover use and predator-related mortality in song and Savannah sparrows. *Auk*, **107**, 775–778.

Werner, E. & Peacor, S. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**, 1083–1100.

Wirsing, A. J. & Heithaus, M. R. 2009. Olive-headed sea snakes (*Disteria major*) shift seagrass microhabitats to avoid shark predators. *Marine Ecology Progress Series*, **387**, 287–293.

Wirsing, A. J., Heithaus, M. R. & Dill, L. M. 2007. Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. *Animal Behaviour*, **74**, 93–101.

Wywialowski, A. P. 1987. Habitat structure and predators: choices and consequences for rodent habitat specialists and generalists. *Oecologia*, **72**, 39–45.