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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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