UNIVERSITY OF CALIFORNIA
SANTA CRUZ

PREDATOR EFFECTS ON MIGRATORY PREY BEHAVIOR, ECOLOGY, AND EVOLUTION

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by

Megan Christine Sabal

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The Dissertation of Megan Sabal is approved:

_____
Professor Eric P. Palkovacs, Chair

_____
Professor Mark H. Carr

_____
Professor Suzanne H. Alonzo

_____
Steven T. Lindley, Ph.D.

_____
Joseph E. Merz, Ph.D.

_____
Peter Biehl
Vice Provost and Dean of Graduate Studies

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Abstract

PREDATOR EFFECTS ON MIGRATORY PREY BEHAVIOR, ECOLOGY, AND EVOLUTION

by

Megan Christine Sabal

Migratory animals are ecologically and economically important and are especially vulnerable to predation. Predators affect migratory prey through both consumption and changes to prey behavior scaling up to affect populations to communities. The balance between consumptive and behavioral predator effects are shaped by risk-reward tradeoffs and ecological constraints. The unique biology of migratory animals results in tradeoffs and constraints involving energetic-demands and optimal timing of migration and traversing heterogeneous and unfamiliar habitats. The goal of my dissertation is to examine how predators affect migrating prey behavior, ecology, and evolution. I used diverse approaches to understand the intersection of predation and migration from fine-scale behavioral decisions up to large-scale patterns among populations and species. In chapter 1, I developed a conceptual framework to predict how migrating prey perceive and respond to predation risk—a direct extension of classic economic escape theory. In chapters 1 and 2, I tested this theory empirically using behavioral assays where I timed juvenile salmon swimming downstream with and without predator cues. In two experiments, juvenile salmon changed behavior

(speed) in response to predator cues, but the pattern of response was context-dependent on previous predator experience and habitat. In chapter 1, wild salmon with more previous predator experience reacted more strongly to predation risk than hatchery salmon. In chapter 2, salmon responded more strongly to predation risk in the shade compared to direct sun and varied their escape strategy—slowing down in the shade and speeding up in the sun. In chapter 3, I conducted a global synthesis across taxa that examines how predators shape animal migrations from behavior to population dynamics to life history evolution. It further explores how humans are disrupting these predator-prey interactions and provides suggestions on how to conserve healthy predation landscapes. Using diverse approaches, from mechanisms to population consequences to ecosystem effects, this work increases our general ecological understanding of predator effects on migratory prey and informs efforts to conserve threatened migratory prey.

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Introduction

Migratory animals are economically and ecologically valuable – connecting distant ecosystems and providing ecosystem services across political boundaries (Semmens et al. 2011). Migrants are often concentrated, conspicuous, and predictable, making them vulnerable to predation and resulting in important and iconic predator-prey interactions (e.g., wolves-elk, orcas-salmon, eagles-shorebirds) (Sabal et al. 2021). Predators can cause migratory prey population declines, which are often exacerbated by human activities (Davis et al. 2012; Furey et al. 2016). Thus, it is important to understand how predators affect migratory prey behavior, ecology, and evolution and the modifying role of human activities.

Predators can affect prey through consumptive and non-consumptive effects, but non-consumptive changes to prey behavior are less examined in migratory prey. Predation risk is well-known to strongly influence behavior in non-migrating prey with cascading ecological consequences on populations and communities (Lima 1998; Preisser et al. 2005). For example, predators can cause prey to spend more time in refuge and less time foraging, thereby reducing growth and survival at later life stages (Matassa and Trussell 2011). In migratory animals, predator induced changes to behavior may scale up and affect migration patterns. As the timing of migration is important for future fitness of migrants, non-consumptive predator effects are an understudied but potentially important mechanism affecting migratory prey populations (Satterthwaite et al. 2014).

Risk-reward tradeoffs and ecological constraints can shape the outcomes of predator-prey interactions (Chamberlain et al. 2014). For example, in non-migrating animals, prey typically face tradeoffs between predation risk and fitness gained through

foraging or mating (Lima 1998). Prey alter their escape responses (e.g. at what distance to flee from a predator) to balance these conflicting demands (Ydenberg and Dill 1986; Samia et al. 2016). Predators may be more effective in consuming prey at human-altered habitats (Sabal et al. 2016). Altered habitats may present an ecological constraint where prey are unable to use normal antipredator behaviors. Migratory prey face unique tradeoffs and constraints, which interact with movement across vast geographic space to shape consumptive and non-consumptive predator effects.

The impact of predation on prey mortality and behavior are highly context dependent (Wirsing et al. 2021). Characteristics of prey, predator, and the environment can influence predation risk, behavioral choices, and mortality. For example, prey in poor condition may choose to face higher predation risk to gain foraging opportunities (Rhoades and Blumstein 2007; Lienart et al. 2014). Habitat can help or hinder the success of predators by providing ambush cover or prey refuge (Ferrari et al. 2013). Environmental attributes (i.e. visibility, temperature, water flow) may also influence predator and prey sensory capabilities, metabolic needs, or physical abilities (Hoover and Richardson 2010). Human activities can drastically shape prey traits, predator communities, and environments, potentially modifying risk-reward tradeoffs and how migrating prey respond to predation risk and resulting mortality.

In this dissertation, I use theory, experiments, and syntheses to examine how predators effect the behavior, ecology, and evolution of migratory prey. In **chapter 1**, I first present a new model variation of economic escape theory to predict how directionally moving prey will respond to risk applicable across taxa. **In chapters 1 and 2**, I apply this framework to field behavioral assays to evaluate how migrating juvenile

Chinook salmon (*Oncorhynchus tshawytscha)* responded to predatory largemouth bass (*Micropterus salmoides)* as modified by salmon origin (hatchery, wild), overhead shade (shade, sun), and structure (present, absent). Juvenile salmon migrate from freshwater to marine environments in spring, where they face high mortality, which is exacerbated by human activities (Buchanan et al. 2013; Demetras et al. 2016). Thus, salmon are an ideal system to explore the non-consumptive effects of predators on migrating prey to inform general ecological theory and evaluate applied consequences. In **chapter 3,** I conducted a review across taxa synthesizing how predators influence migratory prey ecology and evolution, how humans are disrupting these predator-prey interactions, and how to restore healthy predation landscapes. Overall, this dissertation advances our understanding of predator effects on migratory prey with consequences to behavior, populations, and communities.

Chapter 1: An escape theory model for directionally moving prey and an experimental test in juvenile Chinook salmon

Abstract

1. Prey evaluate risk and make decisions based on the balance between the costs of predation and those of engaging in antipredator behavior. Economic escape theory has been valuable in understanding responses of stationary prey under predation risk; however, current models are not applicable for directionally moving prey.

2. Here we present an extension of existing escape theory that predicts how much predation risk is perceived by directionally moving prey. Perceived risk is measured by the extent antipredator behavior causes a change in travel speed (the distance to a destination divided by the total time to reach that destination). Cryptic or cautious antipredator behavior slows travel speed, while prey may also speed up to reduce predator-prey overlap. Next, we applied the sensitization hypothesis to our model, which predicts that prey with more predator experience should engage in more antipredator behavior, which leads to a larger change in travel speed under predation risk. We then compared the qualitative predictions of our model to the results of a behavioral assay with juvenile Chinook salmon (Oncorhynchus tshawytscha) that varied in their past predator experience.

3. We timed salmon swimming downstream through a mesh enclosure in the river with and without predator cues present to measure their reaction to a predator. Hatchery salmon

had the least predator experience, followed by wild salmon captured upstream (wild-upstream) and wild-salmon captured downstream (wild-downstream).

4. Both wild salmon groups slowed down in response to predator cues, while hatchery salmon did not change travel speed. The magnitude of reaction to predator cues by salmon group followed the gradient of previous predator experience, supporting the sensitization hypothesis.

5. Moving animals are conspicuous and vulnerable to predators. Here we provide a novel conceptual framework for understanding how directionally moving prey perceive risk and make antipredator decisions. Our study extends the scope of economic escape theory and improves general understanding of non-lethal effects of predators on moving prey.

Key words: predation risk, antipredator behavior, movement, migration, speed, hatchery, economic escape theory

Introduction

Prey adjust their behavior to balance the tradeoff between predation risk and the costs of engaging in antipredator behavior (Lima and Dill 1990). These predator-induced behavioral decisions are important because they can influence population dynamics and community structure (Werner and Anholttt 1993; Preisser et al. 2005; Matassa and Trussell 2011). Economic escape theory provides a framework to understand this tradeoff (Cooper & Blumstein, 2015; Ydenberg & Dill, 1986). Escape theory has been used to

make predictions about various behavioral responses of prey (e.g. at what distance to flee, when to emerge from refuge) relevant across a range of animal taxa (Martin 1999; Hugie 2003; Cooper and Frederick 2007). The magnitude of the behavioral reaction to predation risk varies based on how much risk prey perceive related to aspects of the predator or environment (e.g. flee at shorter distances when burrows are close by) (Lagos et al. 2009). Therefore, prey behavioral responses to predation risk are also a proxy for how much predation risk prey perceive. Many and diverse empirical tests support patterns from economic escape theory, demonstrating its value in understanding how prey perceive risk and make decisions about antipredator behavior (Stankowich and Blumstein 2005; Stankowich 2008; Samia et al. 2016). All these escape theory models, however, have focused on stationary prey. Animals commonly engage in directional movements that can lead them to encounter predators. Thus, understanding how moving prey assess risk and change their behavior remains an important gap in economic escape theory.

Moving animals are conspicuous and vulnerable to predators (Hammerschlag et al. 2010; Furey et al. 2018). Prey movement can attract the attention of predators, requires energy that reduces the prey's ability to evade an attack, and may occur in unfamiliar space where the location of shelter is unknown (Clarke et al. 1993; Banks et al. 2000). Furthermore, predation pressure on moving animals is often exacerbated by human activities such as introduction of nonnative species and alteration of habitats (Berejikian, Moore, & Jeffries, 2016; MacAvoy, Macko, & Garman, 2001). The only current escape theory model applicable for moving prey was presented by Cooper (2015), and predicts the distance at which a moving prey animal should stop approaching a

stationary predator (nearest approach distance; NAD). However, this model assumes that moving prey will stop their forward movement and will not move past the predator.

There are many directional movements in animal ecology, including migration, dispersal, commuting, patrolling territories, and movements towards or away from a stimulus. In these situations, animals may have a propensity to continue towards a destination regardless of encountering predation risk. Migrating animals must pass by predators encountered *en route* in order to reach their destination—for example, anadromous fish migrating through rivers must pass by relatively stationary predators to reach the ocean (Dalton et al. 2009; Furey et al. 2016). Many animals, such as ants, bats, and penguins, make directional foraging or commuting trips upon which they may encounter predators (Fewell 1990; Ripperger et al. 2015; Poupart et al. 2019). Relevant over many spatial and temporal scales, animals moving toward destinations with a purpose (e.g. water, shelter, food, mates) may encounter areas of predation risk *en route*—for example, dispersing ruffed grouse (*Bonasa umbellus*) (Yoder et al. 2004), diel vertically moving fish (Busch and Mehner 2011), and ungulate movements to and from water sources (Cain et al. 2012). Directionally moving prey include both individual animals traveling in a direct route and those that intersperse travel with temporary pauses and redirection, as long as the overall movement is directional with a destination. Directional movements in animal ecology are common, fundamentally important to fitness, and occur across diverse organisms. Despite moving animals' vulnerability to predators, studies examining how moving prey assess risk and make antipredator decisions are rare and lack a cohesive framework.

The goals of this paper are three-fold. First, we develop a conceptual escape theory model for directionally moving prey—a direct extension of the classic model of Ydenberg and Dill (1986). Second, we use our model to generate qualitative predictions about the sensitization hypothesis, which states that prey with more previous predator experience will react more strongly to predation risk. Third, we test our qualitative predictions based on the sensitization hypothesis in a behavioral assay with migratory juvenile Chinook salmon (*Oncorhynchus tshawytscha*) that vary in their past predator experience.

Adapting Escape Theory to Model Directionally Moving Prey Behavior

Escape response: change in travel speed

Escape theory models focus on predicting optimal escape responses, such as flight initiation distance (FID, the distance at which a prey starts to flee at the approach of a predator) or time to emerge from refuge, to predict a prey's expected reaction to a predator. The prey's escape behavior in different situations can also be used as a proxy for perceived risk. For example, lower FIDs in sheltered versus exposed habitats suggest that prey perceive less risk when shelter is available (de Boer et al. 2004). Likewise, a longer time to emerge from refuge when more conspecifics are present suggests that prey perceive that situation to be riskier, possibly due to predator aggregation in response to prey density (Pezner et al. 2017). The general question escape theory models ask is: how much predation risk do prey perceive? This "perceived risk" is measured as the prey's escape response (or reaction to predation risk). Within an escape theory framework, this

question is applied qualitatively among different situations rather than to make precise quantitative predictions.

Like all animals, directionally moving prey may perceive cues of heightened predation risk and engage in antipredator behavior (Brown, 2003). When moving prey must eventually make it to their destination, engaging in antipredator behavior changes their arrival time (or travel speed). Travel speed is the distance to a destination divided by the total time to reach that destination and can be measured over any spatial or temporal scales. Travel speed differs from instantaneous speed in that some prey antipredator behaviors may increase or maintain instantaneous speed (e.g. fleeing away from the destination, taking an alternative route), but will still delay the prey's arrival to the destination (or slow travel speed).

Examples of antipredator behavior causing changes to travel speed include prey speeding up to reduce their encounter time with comparatively stationary predators relative to the travel speed they would have used if they had not perceived heightened risk (Anderson, Gurarie, & Zabel, 2005; Proffitt et al., 2009). Alternatively, prey may seek cover, increase vigilance, be cryptic, take an alternative route, or wait for less risky conditions (e.g. at night, in turbid water) (Yoder et al. 2004; Cimprich et al. 2005; Ciuti et al. 2012). These cautious or cryptic antipredator behaviors will slow travel speed (or delay time to the destination) compared to if they did not need to use antipredator behavior. Therefore, in our model we can measure directionally moving prey's reaction to predation risk by how much their antipredator behavior changes their travel speed (or time to destination).

Our model considers only changes in travel speed that are caused by antipredator behavior. In the absence of predation risk, animal's travel speed is influenced by many intrinsic and extrinsic factors (Alerstam 2011). For example, prey may travel fast without predator cues as an overall strategy to chronic predation risk, and slow down to increase vigilance when they perceive proximate predator cues, while still traveling quite fast overall. Our model does not predict this "baseline" travel speed, but rather the change in travel speed associated with an antipredator response to a predator encounter. Therefore, in directionally moving prey we can measure the amount of perceived risk (or reaction to a predator) by their change in travel speed via antipredator behavior with and without cues of predation risk.

Cost curves

In economic escape theory, the tradeoff between predation risk and opportunity costs (e.g. missed foraging, mating opportunities) determines prey behavior (Fig. 1a). For directionally moving prey, we assume the cost of changing travel speed (i.e. cost of antipredator behavior) is either energetic (e.g. to fight or flee) or due to mismatched arrival time at the destination. If antipredator behavior delays arrival, animals may lose time engaging in activities, such as foraging or mating, at the destination. Animals could also arrive too early if the purpose at the destination is transient (e.g. seasonal pulses of food or mates). We refer to both the energetic and timing costs of changing travel speed to engage in antipredator behavior as opportunity costs. These opportunity costs increase with the magnitude of the antipredator behavior because prey have larger energetic or timing costs (Fig. 1b).

This model only uses changes to travel speed that are caused by antipredator behavior. Therefore, the cost of not changing travel speed is the cost of no antipredator behavior in the presence of predation risk, which increases the likelihood of being eaten. Therefore, predation risk is at its maximum at no change in travel speed because there is no reaction to predation risk (Fig. 1b). Predation risk is assumed to decrease when prey engage in antipredator behavior, which changes their travel speed (Fig. 1b). If the fitness costs of changing travel speed (opportunity cost) is less than the fitness cost of not changing travel speed (predation risk), then prey should change travel speed to engage in antipredator behavior in response to predation risk. The intersection point between these two cost curves indicates the optimal reaction to predation risk under different conditions. Like all escape theory models, various factors may affect the slopes of either predation risk or opportunity cost curves, resulting in predictions of qualitatively different optimal responses to predation risk, as measured by a change in travel speed.

Thus far, we have focused on how predation risk and opportunity costs affect relative changes in the magnitude of change in travel speed via antipredator behavior (Fig. 1b). In addition, our model can be used to make predictions about the type of escape strategy prey should use because cautious or cryptic antipredator behaviors slow prey down compared to prey speeding up to reduce encounter time with predators (Fig. 1c). For study questions focused only on the amount of risk perceived or in systems where antipredator behaviors are fixed, then modeling unidirectional predictions is appropriate (Fig. 1b). However, prey may have multiple antipredator behaviors, which could cause them to speed up or slow down depending on the situation. In this instance, we can view the graphical model cost curves mirrored around zero change in travel speed (Fig. 1c).

Opportunity costs could be high if prey arrive early or late at their destination, and various antipredator behaviors may minimize predation risk (Brown & Brown, 2000; Saino et al., 2011; Smith & Moore, 2005). If cost curves are symmetrical around zero, then there are two even intersection points, and there could be two optimal antipredator behaviors in different directions. Cost curves, however, are likely not symmetrical. If either cost curve varies in slope between speeding up or slowing down (or between different escape strategies), then there will be two intersection points of varying height (Fig. 1e). For example, if predators are more likely to detect prey if they speed up to flee compared to slow down to be cryptic, then predation risk is higher in the positive direction (Ciuti et al. 2012) (Fig. 1e). Natural selection will favor prey that exhibit the behavior at the lower intersection point, which minimizes fitness costs, and there will be only be one predicted optimal behavior in a particular direction.

Thus, our escape theory model for directionally moving prey can make qualitative and ordinal predictions about two behavioral aspects: (1) the magnitude of change in travel speed infers the amount of perceived risk, and (2) the direction of change in travel speed (speed up vs. slow down) infers the optimal escape strategy. The model can be useful both for generating *a priori* predictions about perceived risk among factors that affect cost curves and *post hoc* understanding of the underlying cost curves based on observed behaviors.

Assumptions and limitations

This model has the same limitations as the other escape theory models discussed in length in Cooper (2015). Mainly, the shape of cost curves may be linear (as shown in

Fig. 1) or curvilinear, and the model is only useful in generating predictions when cost curves intersect. We also assume that antipredator behavior changes travel speed, and there are numerous empirical observations that support this link (Dodson et al. 1997; Proffitt et al. 2009; Hope et al. 2011; Luhring et al. 2016; Melnychuk and Welch 2018). Our model requires directionally moving animals to continue towards a destination and is not applicable if animals permanently stop or change direction. Some of the directional movements we discussed (e.g. dispersal, towards/away from a stimulus) may only fit this categorization in certain situations. When animals permanently or temporarily stop forward movement, the nearest approach distance (NAD) escape theory model (Cooper 2015) can be used, while our model can additionally be used if the prey continues forward movement.

Different from other escape theory models, this model is not exclusive to a single behavior (e.g. FID) and can be applied to various antipredator behaviors (e.g. reduce activity, hide, accelerate), all of which change an animal's travel speed. This feature broadens the model's applicability to different scenarios and species. However, there will always be challenges in connecting complex antipredator behaviors to a single, measurable escape response. Additionally, other escape theory models focus on a single predator interaction (e.g. an organism flees from an approaching predator). Because the escape response for directionally moving prey is a change in travel speed, the cumulative effect from multiple interactions can be observed by examining changes in travel speed (with and without predation risk) over various spatial scales. For example, one could measure a change in travel speed between the presence and absence of a single predator cue (Dodson et al. 1997), or over a migratory bird stopover site (Hope et al. 2011) or total

migration distance as predator density increases (Jonker et al. 2010). A potential consequence of summing behavior changes from multiple predator interactions is for prey to compensate by slowing down to be cryptic followed by speeding up, resulting in no change in travel speed. This effect can be teased apart with experiments at various scales and is important to assess the biological relevance to large behavior patterns.

Sensitization hypothesis

In escape theory models, biological and environmental factors can change the slopes of the predation risk or opportunity cost curves and can lead to qualitatively different predictions about optimal escape behaviors. One example of this is the sensitization hypothesis, which suggests that prey with more previous exposure to predators are more responsive to predator cues from visual, olfactory, and environmental cues (Brown, 2003; Parsons et al., 2018). The prey's ability to assess risk is therefore expected to influence their antipredator behavior. Thus, more experienced prey perceive higher predation risk than less experienced prey, which can be represented by a gradient in slopes of predation risk cost curves (Fig. 1d). The intersections between predation risk and opportunity cost curves qualitatively differ among prey with different prior predator experience. This difference allows testing of the sensitization hypothesis because the magnitude of response to predation risk is expected to vary by previous predator experience. More experienced prey are predicted to exhibit a larger magnitude of change in travel speed (reaction to a predator) compared to less experienced prey (Fig. 1d).

Experimental Methods

We tested the predictions of the sensitization hypothesis based on our escape theory model for directionally moving prey in juvenile Chinook salmon. We timed salmon swimming downstream through a mesh enclosure with and without predator cues to observe their change in travel speed via antipredator behavior. Specifically, we asked (1) do juvenile salmon engage in antipredator behaviors that change their travel speed, and (2) does previous predator experience modify the magnitude of the change in travel speed? We predicted that salmon would change travel speed in the presence of predator cues due to antipredator behavior, and that more experienced prey would react more strongly to predation risk (Fig. 1d).

Study system

Juvenile Pacific salmon (*Oncorhynchus* spp.) face high predation pressure from piscine, avian, and mammalian predators, especially when actively migrating from freshwater to marine environments (Buchanan et al. 2013; Grossman 2016). Many river systems support both naturally-spawned ("wild") and hatchery-reared salmon, which vary in many traits including previous exposure to predators (Huber and Carlson 2015). Salmon raised in hatcheries have no prior exposure to piscine predators, while salmon born in the river have abundant exposure to predator cues (visual, olfactory, and conspecific) and their associations with different situations (Brown et al., 2013; Leduc, Roh, Breau, & Brown, 2007). Additionally, predator experience also increases with distance traveled downstream because moving prey passing stationary predators have increased predator encounter rates with distance traveled (Anderson et al., 2005). Furthermore, piscivore abundance often increase as rivers become larger and warmer downstream (Vannote et al. 1980). We discuss evidence for this gradient of previous

predator experience with downstream salmon movement specific to our study system below. Juvenile salmon are an appropriate study system to apply our escape theory model because they face predation risk and have a propensity for directional movement through both downstream migration and response to local stimuli (e.g. shelter).

We used juvenile Chinook salmon as a test of the sensitization hypothesis through a gradient of previous predator experience from salmon groups differing in origin and location—hatchery (least experience), wild salmon from upstream (wild-upstream; middle experience), and wild salmon from downstream (wild-downstream; most experience). Our conceptual model predicts that wild-downstream salmon should change their travel speed via antipredator behavior with the greatest magnitude under predation risk, followed by wild-upstream, and lastly hatchery salmon (Fig. 1d). Here, we do not make an *a priori* prediction about the direction of change in travel speed because juvenile salmon may either speed up to reduce encounter time (Petersen and Deangelis 2000) or slow down to evaluate risk (Kelley and Magurran 2003; Vehanen 2003).

This experiment spanned 15 – 26 May 2017, and behavior trials were performed on three salmon groups varying in previous predator experience. We used juvenile fall-run Chinook salmon (*O. tshawytscha*) from the lower Mokelumne River, CA. Salmon eggs hatch in late winter and juvenile salmon downstream migration occurs within five months when salmon are between 35 – 120 mm fork length (FL) (Merz et al. 2013). All salmon used in our experiments were of migratory sizes (55 – 110 mm FL) and tested during peak migration. Hatchery salmon were obtained daily from the Mokelumne River Fish Hatchery where hatchery salmon are managed as the same genetic population as wild salmon (Williamson and May 2005). Wild salmon were obtained from two

locations. Upstream, wild salmon (wild-upstream) were captured by pulling a seine (7.6 m-long, 1.5 mm mesh) on a floodplain adjacent to the enclosure site. Forty-one river km downstream, wild salmon were captured by a rotary screw trap (2.4 m in diameter; E.G. Solutions, Inc.) operated by East Bay Municipal Utility District (wild-downstream). Wild salmon were typically captured on a single day at the beginning of the week and were held in small live bins in the river for 1-3 days until being run in behavioral trials. Traveling from upstream to downstream capture locations, juvenile salmon on the Lower Mokelumne River encounter an increasing abundance of nonnative predators (including largemouth bass) as measured by fish community surveys (Del Real et al. 2018). Additionally, wild-downstream salmon have passed through a known predator hotspot at the Woodbridge Irrigation District Dam where striped bass (*Morone saxatilis*) congregate and prey heavily on juvenile salmon, while wild-upstream salmon have remained in habitats with lower predator abundance (Sabal et al. 2016). Salmon groups also varied in physical traits (length, weight, condition factor, ATPase) due to age and rearing histories (Appendix S1). To test the sensitization hypothesis with our economic escape theory model, we focus only on the gradient of previous predator experience, but we describe trait differences among salmon groups and we found that trait differences among salmon groups did not appear to affect overall travel speed or reaction to predation risk in Appendix S1. All handling and procedures were approved under Institutional Animal Care and Use Committee (IACUC) protocol PALKE1701.

Behavioral assay

To empirically test predictions from our conceptual escape theory model, we designed an experiment to accentuate directional prey movement and manipulated predator cues to measure a change in travel speed via antipredator behavior. We recorded how long it took juvenile Chinook salmon to swim downstream through a mesh enclosure in the river with and without predator cues present. In May 2017, an enclosure created with two layers of 76 micron-fine mesh was placed in the lower Mokelumne River on a floodplain in 0.3 m-water depth. Flows were very low (mean surface velocity: 0.2 m/s ± 0.06) and did not prevent salmon from stopping, slowing down, or turning around in the enclosure. The enclosure started with a constricted end of 0.1 m diameter, gradually increased to 0.45 m diameter at distance 1.2 m and continued for a total distance of 2.4 m (Fig. 2). The enclosure had no substrate, was completely submerged underwater parallel to downstream flow and entered a net pen. Three Passive Integrated Transponder (PIT) tag antennas were placed around the outside of the enclosure at distances 0.3 m, 1.2 m, and 2.1 m from the starting end (hereafter referred to as antenna A1, A2, and A3 respectively). We therefore timed salmon swimming through two splits: from A1 to A2, and from A2 to A3. In predator trials a model predator (described below) was placed at antenna A2. Therefore, split A1 to A2 represents moving towards the predator and A2 to A3 moving away from the predator.

The behavioral assay required salmon to swim repeatedly downstream to observe the change in travel speed with predator cues present. To reinforce their migratory propensity to move downstream, we assumed salmon should want to move away from conspecific alarm cues and towards habitat structure. Therefore, we provided conspecific alarm cues, from five shallow vertical cuts on one live and one euthanized salmon, at the

upstream end of the enclosure and placed simulated vegetation (plastic aquarium plants) at antenna A3 to encourage downstream movement (Anderson & Mathis, 2016). For trials with predator cues, we placed a plastic replica of a largemouth bass (*Micropterus salmoides*) (length 30.5 cm), a known predator of juvenile salmon in this river, into the middle of the enclosure at antenna A2. To simulate olfactory predator cues, we pureed two largemouth bass fillets and four euthanized hatchery Chinook salmon with vegetable shortening and spread a thin layer of this mixture onto the bass replica prior to predator trials. The combination of conspecific alarm cues and predator odor cues are commonly used indicators of predation risk in behavior experiments (Ferrari et al. 2007). The enclosure design precluded some juvenile salmon natural antipredator behaviors, such as schooling, hiding in substrate, and movements perpendicular to flow, but did allow predator inspection, vigilance, and cautious behavior, which are common fish antipredator behaviors over small spatial and temporal scales (Kelley and Magurran 2003).

Prior to behavior trials, each salmon was anesthetized in a non-lethal dose of MS-222 (0.2 g/L) buffered with $NaHCO_3$ (2 g/L), weighed, measured (FL), and injected with a HDX12 PIT tag (12 mm x 2.12 mm, 0.1 g) into the body cavity with a handheld syringe-style implanter. All salmon were below the 6.7% tag burden limit which may affect survival (mean ± SD: 1.5 ± 0.8%) (Brown et al., 2010). All salmon were allowed at least 30 minutes to recover after tagging, but all recovered within a few minutes, and there were no tagging mortalities. To begin a behavior trial, a single salmon was selected randomly and placed in a perforated plastic container and set in the upper part of the enclosure and allowed to acclimate for one minute. At that time, the container lid was

removed, and the container was rotated 90 degrees, so the opening faced downstream. Timing did not begin until the salmon moved downstream and was detected by the first antenna. The trial ran until the salmon reached antenna A3 or at 10 minutes whichever came first. We switched predator and no predator trials every two salmon. At the end of the first round, trials were repeated for the same salmon, selecting fish randomly, and running the appropriate predator cue treatment, so that each salmon was run with and without predator cues. At the end of each trial day, hatchery salmon were euthanized with a lethal dose of MS-222 (0.6 g/L), and wild salmon were released back into the river. Environmental conditions were recorded daily including water temperature, air temperature, surface water velocity, turbidity, and cloud cover.

Data analysis

To evaluate our study questions, namely (1) do juvenile salmon change their travel speed under predation risk and (2) does previous predator experience modify the magnitude of the change in travel speed, we observed if travel speed was influenced by the interaction between predator cue presence and salmon group. We used a mixed-effects Cox regression because it uses censored data over time—both measures of an event (salmon reaching an antenna) happening or not (0,1) and the time at which that event occurred. Therefore, the Cox model response represents travel speed, as it measures the probability of reaching antennas (traveling a set distance) over time and uses data from all salmon including fish that failed to reach antenna A2 or A3 in the allotted 10 minutes. Analyses were conducted using the ‘coxme’ R package (Therneau 2015).

The model included three fixed effects and their two-way interaction (predator cues [present, absent], salmon group [hatchery, wild-upstream, wild-downstream], and split [A1-A2, A2-A3]). We included split because it is a main component of our enclosure design and we wanted to account for potential impacts to salmon behavior. We included individual salmon as a random effect to account for paired trials. We subsequently performed a Type III ANOVA on the Cox model to assess covariate significance. We used linear contrasts using the R package 'lsmeans' (Lenth and Love 2017) to determine post-hoc differences in reaction to predation risk between salmon groups. We calculated effect sizes (Hedge's g) using the R package 'effsize' (Torchiano 2017), and interpreted magnitude of effects following the thresholds $|g| < 0.2$ "negligible", $|g| < 0.5$ "small", $|g| < 0.8$ "medium", $|g| > 0.8$ "large" (Cohen 1992). We also replicated the above analyses using both travel speed (m/s) and body lengths per second (bl/s) on the truncated dataset excluding salmon that did not reach antennas. We used linear-mixed effects models on the response variables speed (m/s and bl/s) and observed congruent results (see Appendix S2).

We also confirmed that non-target covariates did not affect salmon's reaction to predation risk. We used linear regressions to assess the influence of time of day, time between trials, and order of predator treatments on travel speed to account for trials occurring between 9:00 and 15:00 and because salmon were chosen randomly for their second trial, thus varying the time between predator and no predator treatments. These models also included predator treatment as a covariate because we were only interested in the potential significance of the interaction between the non-target variable and predator treatment on travel speed. We summarized salmon physical traits by salmon group and

assessed if traits affected reaction to predation risk; our results suggest they did not (Appendix S1). Patterns in travel speed among salmon groups and split (not related to our escape theory model predictions) are presented in Appendix S3 (Table S4).

Experimental Results

We ran 63 juvenile Chinook salmon through paired behavior trials (n = 126), using both hatchery (n = 24) and wild salmon (wild-upstream n = 20; wild-downstream n =19). Environmental conditions were relatively consistent over the study period: water temperature (mean: 15.2 ºC ± 0.3), air temperature (mean: 27.8 ºC ± 5.2), surface water velocity (mean: 0.2 m/s ± 0.06), and turbidity (mean: 1.2 NTU ± 0.4). There were no significant relationships with salmon travel speed and reaction to predation risk with any non-target variables including: time of day (linear regression: t = 1.36, p = 0.18), time between trials (t = -0.21, p = 0.84), or order of predator treatments (t = 0.76, p = 0.45). Salmon physical traits did not relate to travel speed or reaction to predation risk within salmon groups (Appendix S1).

Salmon reached antenna A2 in 93.7% of trials, on average in 84 ± 127 s or traveling at 0.05 ± 0.05 m/s. In only 39.7% of trials salmon reached antenna A3 because many salmon stopped moving when they reached the aquatic vegetation before they were detected at A3. The average time from antenna A2 to A3 was 129 ± 134 s or traveling at 0.04 ± 0.06 m/s. Travel time was highly right-skewed with most salmon traveling quickly through the enclosure (Fig. S1). There were significant interactions between predator treatment and salmon group and between split and salmon group influencing salmon travel speed (Fig. 2; Table 1). Hatchery salmon did not change travel speed between

predator treatments (Table 2), moving downstream in a similar time regardless of predator cues. In contrast, wild-downstream and wild-upstream salmon slowed down 42.8% (linear contrasts: Z-ratio = 3.46, $p < 0.001$, n = 76) and 33.3% (Z-ratio = 1.88, $p = 0.06$, n = 80) respectively, when predator cues were present (Fig. 2; Table 2). Therefore, the magnitude of reaction to predator cues by salmon group followed the gradient of previous predator experience and the sensitization hypothesis.

Discussion

Here we first develop a conceptual model, based on escape theory, for understanding escape decisions by directionally moving prey. This model is based on the idea that directionally moving prey will engage in antipredator behavior when they perceive predation risk that will cause them to change travel speed. Consistent with our model, juvenile salmon changed travel speed due to antipredator behavior and the relative magnitude of the reaction supported the sensitization hypothesis. Wild salmon (with prior predator experience) reacted to predation risk, while hatchery salmon (without prior predator experience) did not change travel speed in response to predator cues. We did not have an *a priori* prediction for which direction salmon would change their travel speed, but our empirical results showed that wild salmon slowed down when they were exposed to predator cues. This observation suggests salmon's escape strategy was to slow down to evaluate risk instead of to speed up to reduce predator encounter time. Our escape theory model provides a common framework to understand tradeoffs that influence how directionally moving prey respond to predation risk and to make qualitative predictions about behavioral patterns across ecosystems and taxa.

Wild juvenile salmon changed travel speed in response to predation risk, supporting the prediction that antipredator behavior affects travel speed in directionally moving prey. Many antipredator behaviors can cause a change in travel speed. In this study, juvenile salmon appeared to slow down because they were evaluating risk through predator inspection or increased vigilance, which are common antipredator behaviors in fish (Kelley and Magurran 2003). Observationally, juvenile salmon would often swim towards the model predator and then circle back upstream before reaching A2 appearing to gather information. These inspecting movements slowed total time through the enclosure and illustrate how instantaneous speed differs from travel speed. Other studies have also observed the connection between predation risk and travel speed in various taxa at different scales. For example, in small-scale experiments that manipulated predator cues, zooplankton (*Daphnia hyalina*) and sea lamprey (*Petromyzon marinus*) increased their travel speed, presumably to reduce encounter time with predators (Dodson et al. 1997; Luhring et al. 2016). At larger scales, forest birds translocated away from their home territories, travelled more slowly returning home as forest cover decreased, perhaps because birds took longer routes to avoid large gap crossings with high predation risk (Bélisle et al. 2010). Juvenile sockeye salmon (*O. nerka*) had slower travel rates in river reaches with clear water (high risk from visual predators) by pausing to migrate nocturnally relative to turbid reaches (low risk) (Clark et al. 2016). Strategic punctuated movements of fast and slow speeds differ from antipredator behaviors that slow travel rate more consistently, but both can slow overall travel speed. Therefore, measuring the change in travel speed in directionally moving prey as an escape response has broad

applicability across antipredator behaviors, species, and scales to understand patterns in perceived risk.

The relative magnitude of the observed reaction to predation risk in our experiment followed the predictions of the sensitization hypothesis, which suggests prey with more previous predator experience will react more strongly to predation risk. Wild-downstream salmon had the most prior predator experience and the greatest change in travel speed, followed by wild-upstream and lastly, hatchery salmon. Prior work has shown that hatchery conditions can alter salmon brain development, locomotion, aggression, and perception of risk resulting in maladaptive responses to predators and heightened mortality once released (Sundström et al. 2004; Kihslinger and Nevitt 2006; Hawkins et al. 2008). These various effects may explain why hatchery salmon did not respond to the presence of predator cues. With the immense contribution of hatcheries to salmon populations (Barnett-Johnson et al. 2007), it is important to understand how rearing environment and exposure to predator cues change antipredator behavior. Overall, this experiment demonstrates how an economic escape theory approach can be applied to directionally moving prey mirroring the application of other escape theory models to stationary prey (Hoover and Richardson 2010; Shannon et al. 2016; Parsons et al. 2018).

We did not directly manipulate the individual history of previous predator experience but instead relied on a natural (and anthropogenic) gradient. Thus, our experiment cannot differentiate between the effects of predator experience and other mean trait differences among salmon groups or interactions with the different environments upstream and downstream on the reaction to predator cues (Appendix S1). However, many predator conditioning experiments with hatchery salmon show improved

behavioral responses and survival, suggesting lack of individual predator experience is critical for shaping responses to predation risk (Alvarez, Nicieza, & Oviedo, 2003; Berejikian, Smith, Tezak, Schroder, & Knudsen, 1999; Jackson, Brown, & Fleming, 2011; Roberts, Taylor, & Garcia De Leaniz, 2011). Additionally, the reaction to predation risk among salmon groups did not follow patterns of mean size, body condition or migration propensity (ATPase) (Appendix S1). Neither did those traits influence reaction to predation risk within salmon groups (Appendix S1).

Our conceptual model is also useful in inferring prey's escape strategy based on the direction of change in travel speed (speed up vs. slow down). In our experiment, predator cues caused wild salmon to slow down both on the approach (A1 to A2) and beyond (A2 to A3) the model predator. Slowing down suggests that juvenile salmon's antipredator strategy may have been to evaluate risk in the vicinity of predator cues regardless of position relative to the cue. Alternatively, salmon may have slowed down from A2-A3 when the predator was present by seeking shelter in the aquarium plants. Prey may evaluate risk through increased observation, vigilance, and predator inspection to accurately assess risk to choose the optimal reaction to predation risk that avoids fitness costs of reacting more than necessary (Sih and McCarthy 2002; Sutton and O'Dwyer 2018). Gathering new information takes time and energy, and in moving animals, this could slow travel speed—for example, when increased vigilance at stopover sites delays refueling and subsequently travel speed in migratory birds (Hope et al. 2014).

Behavioral assays are valuable to test specific hypotheses; however, there are challenges to connecting small-scale experiments to natural phenomena. In this study, our experimental enclosure excluded some natural juvenile salmon antipredator behaviors,

and important next steps include applying our model to more natural settings. Broadly relevant to the escape theory model, habitat complexity, environmental conditions, and biological communities can interact to affect predation risk, and no assay can account for all variables (Lank & Ydenberg, 2003). However, our model provides a framework to test different aspects of the environment, predator, and prey in different experiments. Spatial scale is also important in interpreting study results because measuring travel speed over both low and high predation risk areas together could obscure specific behaviors. Also, prey behavior from multiple predator encounters can only be observed over larger spatial scales if they are consistent over space and time. Prey may compensate for slowing down in high-risk areas by speeding up in low-risk areas, resulting in no net change in time to the destination. For example, when predation risk is high, a migrant may alternate between temporarily hiding and fleeing towards the destination, using a mix of antipredator behaviors that speed up and slow down travel speed. In this situation and others, there will always be challenges in simplifying complex antipredator behaviors to a single, measurable escape response. Despite these challenges, examining prey behavior at various scales is important to understand the biological relevance to larger-scale phenomena, for example dispersal or migration (Middleton et al. 2013). Our conceptual model can be used over various scales and antipredator behaviors; therefore, the framework exists to tease apart behavioral mechanisms resulting in a more complete picture of escape decisions and their consequences.

In addition to short-term antipredator responses to proximate predation risk, moving prey may also exhibit behaviors adapted to chronic predation risk. Animals can migrate in groups to dilute risk (Reynolds et al. 2009; Armstrong et al. 2016; Furey et al.

2016) and follow specific routes to avoid predators (Ydenberg, Butler, & Lank, 2007). These are general evolved strategies that are not initiated by proximate predator cues. Prey commonly use behaviors adapted to overall risk (e.g. move in groups) and proximate risk (e.g. vigilance) at the same time. For example, juvenile salmon may benefit from traveling fast to reduce predator-prey overlap as a general strategy, but when they perceive cues indicating reaches of high local risk, they may slow down to migrate nocturnally or evaluate risk (Clark et al. 2016). This layering of strategies may contribute to the inconsistent patterns observed between juvenile salmon travel speed and survival at broad scales (Hockersmith et al., 2003; Muir, Smith, Williams, Hockersmith, & Skalski, 2001; Smith, Muir, Williams, & Skalski, 2002). Our conceptual framework can help in designing experiments that isolate proximate responses and testing the modifying effects of ultimate strategies. For example, one could hypothesize that prey moving in groups perceive less predation risk (lower cost curve) and, therefore, should change travel speed less compared to solitary prey due to proximate mechanisms. These types of studies may help explain inconsistent patterns observed at large scales by understanding context-dependent decisions of directionally moving prey.

Economic escape theory models have been valuable to understand how much risk prey perceive (Cooper and Blumstein 2015). Behavioral responses under predation risk are important because they can subsequently affect populations and communities (Preisser et al. 2005; Matassa and Trussell 2011). Here, we developed an escape theory model variation for directionally moving prey. Moving animals are vulnerable to predation and understanding how these prey perceive risk and make antipredator decisions will help to evaluate non-consumptive predator effects. Changes to travel speed

from antipredator behaviors may have direct physiological costs or indirect fitness costs due to a mismatch in destination arrival time, both which may affect survival in later life stages (Peterson 1976; Saino et al. 2011). Understanding predator effects on directionally moving prey behavior advances economic escape theory and improves our general understanding of how animals assess predation risk.

Authors' contributions: MCS, EPP, and JEM designed the study. MCS ran the experiment and performed analyses. MCS and SHA developed the conceptual model. MCS wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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Data Accessibility:

Data available from the Dryad Digital Repository: https://doi.org/10.7291/D1Q37T (Sabal et al. 2020).

Supporting Information:

Appendices S1-S3 (Available online: jane13233-sup-0001-Supinfo.docx)

Figures & Tables

Table 1.1 Linear contrasts and effect sizes on salmon speed (time to event) upon significant interactions between salmon origin-life stage with predator treatment and split.

Covariates	COXME: speed	
	χ^2	p
Predator	0.25	0.62
Split	0.07	0.80
Salmon group	15.89	0.0004*
Predator x Split	0.04	0.85
Predator x Salmon group	8.34	0.02*
Split x Salmon group	11.03	0.004*
† p < 0.1, * p < 0.05	*n trials x split (252)*	
	n salmon (63)	

Table 1.2 Linear contrasts and effect sizes on salmon speed (time to event) upon significant interactions between salmon origin-life stage with predator treatment and split.

Salmon group	COXME: speed		Effect Size	
	Z-Ratio	p	Hedge's g	Magnitude˚
Predator treatment				
Hatchery	-0.38	0.71	0.12	negligible
Wild-upstream	1.88	0.06†	-0.38	small
Wild-downstream	3.46	< 0.001*	-0.62	medium

† $p < 0.1$, * $p < 0.05$, ˚ thresholds defined by (Cohen 1992)

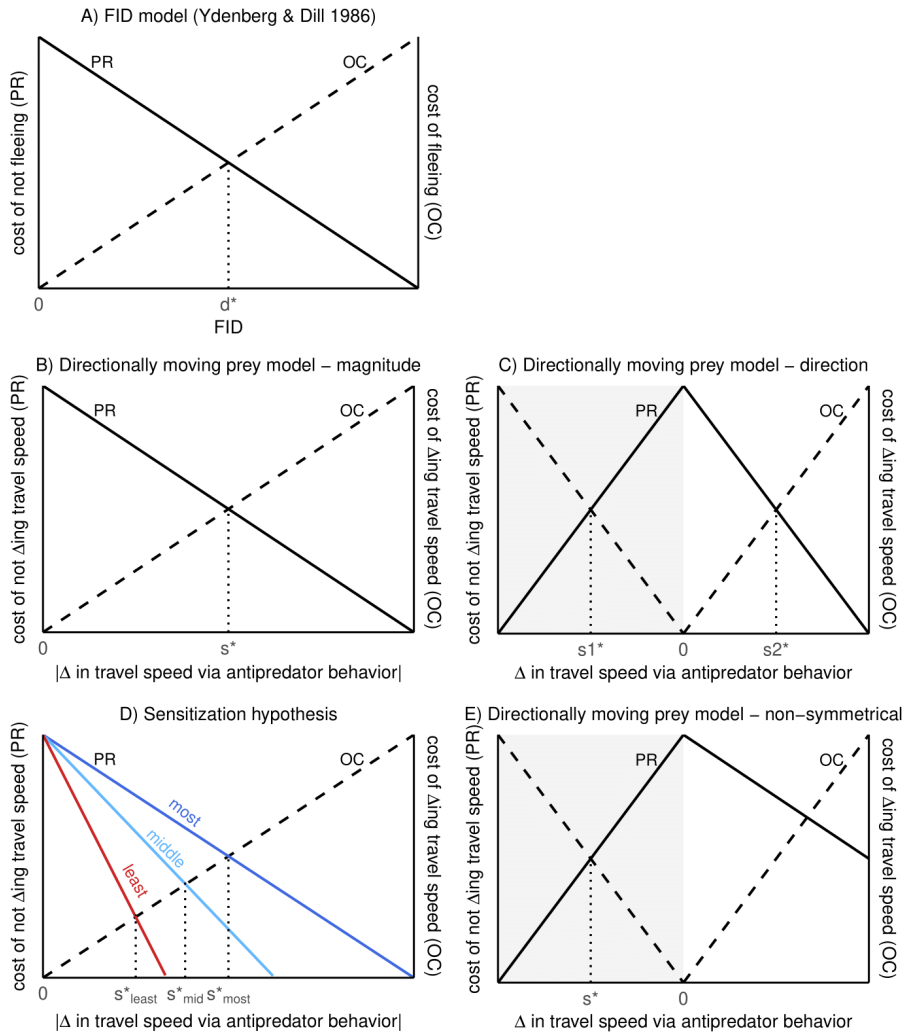

Figure 1.1 Economic escape theory models including, A) classic model from Ydenberg and Dill (1986) predicting flight initiation distance (FID), and model for directionally moving prey predicting the change in travel speed for B) magnitude only, C) magnitude and direction, D) the sensitization hypothesis (most, middle, least previous predator experience), and E) when cost curves are not symmetrical around zero. The costs of fleeing and not changing travel speed are proxies for predation risk (PR; solid lines), while the costs of not fleeing and changing travel speed are proxies for opportunity costs (OC; dashed lines). Variables with asterisks indicate optimal behaviors at intersection points.

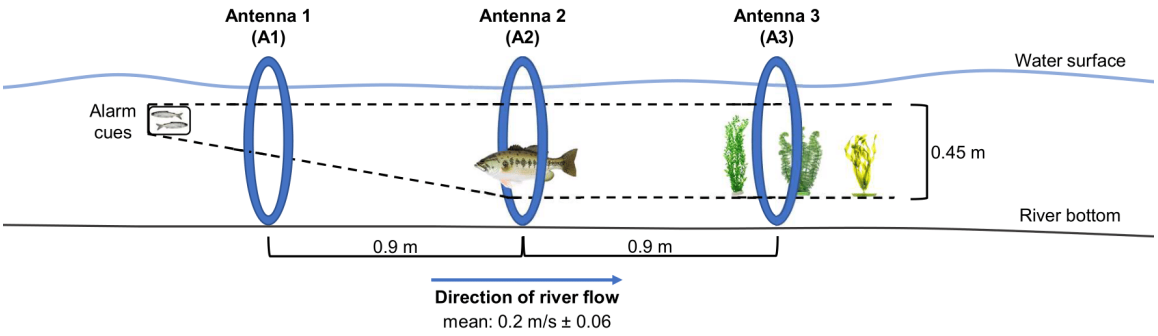

Figure 1.2 Diagram of experimental mesh enclosure including positions of antennas, model predator (at A2), conspecific alarm cues (before A1), and artificial habitat (at A3). Juvenile salmon were released between the alarm cues and antenna A1.

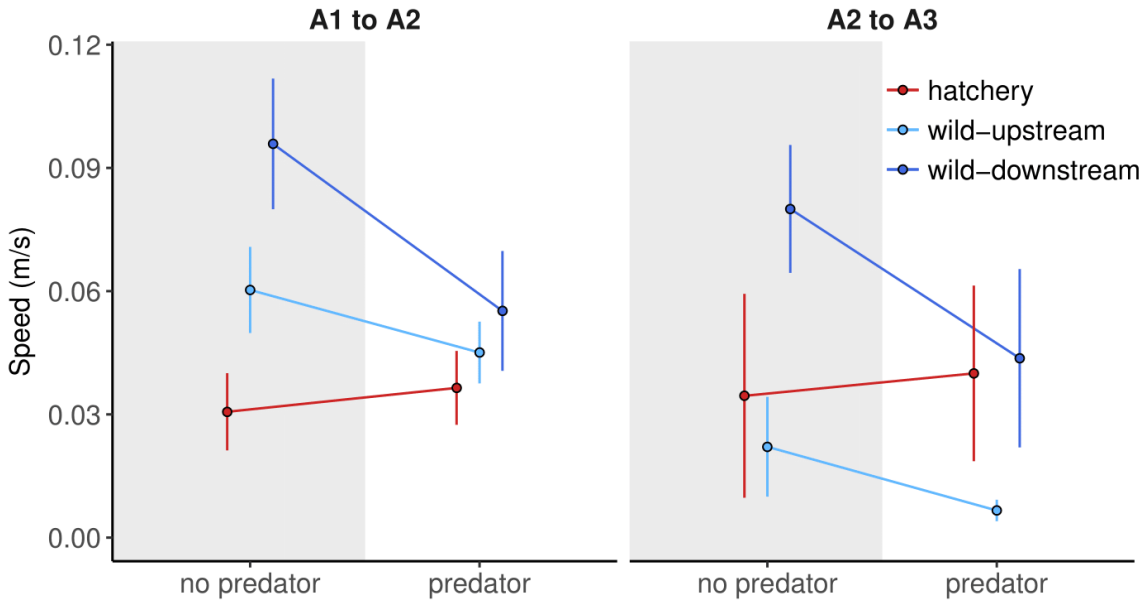

Figure 1.3 Reaction norms showing changes in mean salmon travel speed (m/s) between no predator and predator cue trials. The left plot represents changes in travel speed by predator cues in the first half of the enclosure between antenna A1 to A2, while the right plot shows travel speed changes from A2 to A3. Vertical lines represent standard errors.

Chapter 2: Shade affects magnitude and tactics of juvenile Chinook salmon antipredator behavior in the migration corridor

Abstract

Environmental conditions strongly affect antipredator behaviors; however, it is less known how migrating prey adjust antipredator behavior in migration corridors, in part, because active migrants are difficult to observe and study. Migrants are vulnerable and encounter many predators in the corridor, and their propensity to travel towards their destination ties antipredator behavior with movement. We evaluated how environmental risk cues in the migration corridor including in-water habitat structure (present, absent) and overhead shade (sun, shade), and salmon origin (hatchery, wild) affected how juvenile Chinook salmon (*Oncorhynchus tshawytscha*) reacted to a live predator. We measured how salmon react to predation risk as the difference in time to swim downstream through a 9.1-m long field enclosure with or without a live predatory largemouth bass (*Micropterus salmoides*). Shade significantly modified the reaction to the predator, and it did so in two ways. First, the magnitude of antipredator behavior was larger in shade compared to direct sun, which suggests salmon perceived shade to be a riskier environment than sun. Second, the escape tactic also varied; salmon slowed down to be cautious in shade and sped up in sun. Structure did not significantly affect behavior and hatchery and wild salmon behaved similarly. Our study suggests that environmental risk cues can shape the magnitude and tactics of how migrants react to predation risk and illustrates how these responses relate to movement with potential to scale up and affect migration patterns.

Key words: movement, predation risk, light, structure, refuge

Introduction

Prey use environmental cues to assess predation risk and adjust their antipredator behavior (Lima and Dill 1990). For example, animals often perceive sheltered habitats to be less risky than exposed habitats, and consequently, in sheltered habitats prey allow predators to approach more closely before they flee (de Boer et al. 2004). Habitat-dependent antipredator behavior has been heavily studied in resident prey and can scale up to affect populations and communities (Preisser et al. 2005; Wirsing et al. 2021). However, these antipredator decisions are much less studied in migrating animals, despite that migrants often experience high predation risk in migration corridors where they are concentrated and conspicuous (Furey et al. 2018). Furthermore, antipredator behavior in the migration corridor affects fine-scale movement creating a potential pathway to affecting migration duration or arrival time (Hope et al. 2014; Sabal et al. 2020). Migratory prey are economically and ecologically valuable and, thus, it is important to examine their context-dependent antipredator behavior in the risky migration corridor.

Habitat structure is a powerful environmental driver of prey antipredator behavior. Structure commonly decreases predation rates because it disrupts visual hunting by predators and provides prey refuge (Crowder and Cooper 1982; Allouche and Gaudin 2001; Bonnot et al. 2016). Consequently, animals engage in less antipredator behavior when closer to refuge (e.g. wait longer to flee from an approaching predator, be less vigilant) (Frid 1997; Anibal Stellatelli et al. 2015). Structure can also cause prey to

shift escape tactics. For example, bluegill sunfish (*Lepomis macrochirus*) evaded largemouth bass (*Micropterus salmoides*) by hiding when structure was present and by schooling when structure was absent (Savino and Stein 1982). Therefore, structure may influence the magnitude and escape tactics of migrating prey. However, in migration corridors local habitat structure is less familiar to transient migrants compared with local habitats of resident prey, which could alter migrant behavioral responses to structure in the corridor (Forrester et al. 2015; Moore 2018).

Shade during daylight influences antipredator decisions commonly across taxa and is relevant to antipredator decisions on a similar scale as habitat structure. For many organisms, shade indicates low risk because it provides cover, is often correlated with structure, and reduces glare, which improves detection of predators (McMahon and Hartman 1989; McCartt et al. 1997; Mandelik et al. 2003; Carr and Lima 2014). Therefore, we might expect prey to exhibit lower intensities of antipredator behavior in shade. For example, house finches (*Carpodacus mexicanus*) perceived shade to be less risky than sunlight and reduced their antipredator response to predation risk in shade (e.g. reaction time, scanning behavior) (Fernández-Juricic and Tran 2007). However, shade may also indicate high risk. Overhead shade that is not associated with structure, including anthropogenic structures (e.g. docks, bridges), may cause prey avoidance in fish (Able et al. 2013; Nebel et al. 2019). Additionally, low light can decrease prey vision and reduce information about the predator and environment, increasing perceived risk (Cerri 1983; Leahy et al. 2011). Migrants encounter many predators across an environmentally-variable migration corridor with shade from natural and anthropogenic sources with the potential for shade to indicate low or high risk.

Juvenile Pacific salmon (*Oncorhynchus* spp.) encounter numerous predators as they migrate from freshwater to marine environments (Rieman et al. 1991; Evans et al. 2012; Thomas et al. 2017). When rearing upstream, salmon use structure and shade from riparian vegetation, which often covers much of the stream channel, to hide from predators (McMahon and Hartman 1989; Reinhardt and Healey 1997; Korstrom and Birtwell 2006; Penaluna et al. 2015). However, when salmon migrate through the larger rivers of the migration corridor, the role of habitat mediating predation risk is unclear. Habitat structure, including woody debris and submerged aquatic vegetation, has been presumed to both decrease predation risk by providing prey refuge and increase predation risk by providing predator habitat (Zajanc et al. 2013; Henderson et al. 2019). Migrating juvenile salmon also can have a variable reaction to shade – they may avoid passing through shade cast by anthropogenic structures, but also preferentially hold in shaded reaches with complex habitat (Kemp et al. 2005; Zajanc et al. 2013; Ono and Simenstad 2014; Hellmair et al. 2018). Habitat structure and shade are more constrained to the shoreline in the migration corridor.

An additional element likely influencing juvenile salmon antipredator behavior is the role of fish hatcheries. Hatchery salmon often differ in genetics, morphology, physiology, and behavior compared to salmon born in the river ("wild salmon") (Weber and Fausch 2003; Jonsson and Jonsson 2006). Hatchery salmon lack prior predator exposure, which may cause them to react less to predation risk than wild salmon (Alvarez et al. 2003; Roberts et al. 2011). Overall, migrating juvenile salmon encounter many predators and habitats potentially associated with different risk levels, while hatchery influence may further affect salmon antipredator behavior.

To examine antipredator decisions in the migration corridor, we need to measure a behavioral reaction to predation risk and observe how that reaction changes under different contexts. When prey react more strongly to a predator, for example in exposed compared to sheltered habitats, we can assume the prey perceived higher predation risk (Ydenberg and Dill 1986; Camp et al. 2012). Since migrating prey have a propensity to travel in a set direction, we can assess their reaction to predation risk by measuring how much they adjust their travel speed (or time to destination) to engage in antipredator behavior (Sabal et al. 2020). Cryptic and cautious antipredator behavior in migrants slows travel speed—for example, increasing vigilance, hiding in cover, and punctuated movements (Chung et al. 2009; Hope et al. 2014; Melnychuk and Welch 2018). Alternatively, migrants may speed up to reduce encounter time with comparatively stationary predators (Peterson 1976; Proffitt et al. 2009). Therefore, how much prey adjust their travel speed indicates the magnitude of perceived predation risk, while the direction that prey change their travel speed relates to their escape tactic.

We performed a behavioral assay with juvenile Chinook salmon (*O. tshawytscha*) to measure the difference in downstream travel speed with and without a predatory largemouth bass (*Micropterus salmoides*) present (i.e., their reaction to a predator). We observed two aspects of the antipredator response—the magnitude (amount of perceived predation risk) and direction (escape tactic) of the change in travel speed. We evaluated context-dependence of salmon antipredator responses by varying structure (present, absent), shade (sun, shade), and salmon origin (hatchery, wild). Specifically, we asked (1) do migrating salmon change their travel speed in response to the presence of a predator,

and (2) how do structure, shade, and salmon origin modify the magnitude and direction of their change in travel speed?

We predicted that salmon would change their travel speed to engage in antipredator behavior in response to predator presence. For the magnitude of antipredator response, we predicted that structure and shade would modify perceived predation risk. However, we did not make an *a priori* prediction as to whether the presence of structure or shade would increase or decrease the reaction to the predator because of conflicting prior evidence and the knowledge that animals in the migration corridor may respond to environmental risk cues differently than when not migrating (Zajanc et al. 2013; Ono and Simenstad 2014; Henderson et al. 2019). We predicted that wild salmon would react more strongly to a predator compared to hatchery salmon because of increased prior predator experience (Roberts et al. 2011; Solberg et al. 2020). We did not make an *a priori* prediction as to the escape tactic because salmon may slow down to evaluate risk or speed up to reduce encounter time with relatively stationary predators (Petersen and Deangelis 2000; Vehanen 2003; Sabal et al. 2020).

Materials and methods

We performed 144 behavioral assays on juvenile fall-run Chinook salmon between 02-May-2018 and 31-May-2018. We measured the magnitude of antipredator behavior as the difference between the mean travel speed without the predator and the mean travel speed with the predator present. The difference in travel speed can be caused by various antipredator behaviors, such as fleeing, predator inspection, reducing activity,

and temporarily hiding (Sabal et al. 2020). Trials occurred on the lower Mokelumne River, California—a part of the migration corridor.

Study site

The experiment's location on the lower Mokelumne River (38.202957° N, -121.516989° W) sits approximately 41 river-km downstream from salmon spawning locations and 130 km upstream of the Pacific Ocean. When migrating juvenile salmon reach the study area, they encounter relatively low water velocities that change direction due to tidal influence (range: -0.3 to 0.4 m/s). We only performed trials during outgoing tides when salmon are more likely to travel downstream (Hering et al. 2010). Juvenile Chinook salmon have a propensity to migrate nocturnally; however, diel movements also occur and increase in frequency in the Sacramento-San Joaquin Delta compared to upstream reaches (Chapman et al. 2012). River turbidity at our study site was relatively low (mean + sd: 3.48 ± 1.13 NTUs) and likely would not strongly affect reaction distances between predator and prey (Miner and Stein 1996). The river is bordered by leveed banks with riprap and occasional trees, which cast shade onto the river margins on clear days. Woody debris and submerged aquatic vegetation are occasionally present along this stretch of the lower Mokelumne River.

Juvenile salmon and largemouth bass

We used hatchery and wild juvenile Chinook salmon to examine how salmon origin affects antipredator decisions. Hatchery salmon were obtained from the Mokelumne River Fish Hatchery where hatchery and wild salmon are managed as a

single gene pool (Williamson and May 2005). Therefore, any behavioral differences in hatchery salmon in our experiment are presumably from altered rearing conditions. Wild salmon were obtained from a rotary screw trap (2.4 m in diameter; E.G. Solutions, Inc.) operated by East Bay Municipal Utility District. The screw trap was operated 35 river km upstream of the study site and only captures actively migrating salmon. Both wild and hatchery salmon were obtained weekly and held in coolers with aeration on site until they were run in trials (days since capture, range: 0 to 4 days). Largemouth bass (n = 19) were obtained from nearby locations through boat electrofishing and hook-and-line sampling and were held in 1135 L-tanks on site for the entire month of experiments. We weighed, measured fork length (FL), and calculated Fulton's condition factor (K) of juvenile salmon. Largemouth bass FL ranged from 198 – 326 mm and were all capable of consuming juvenile salmon (66 – 109 mm FL) (Hambright 1991; Michel et al. 2018). External anchor tags (Floy Tag, Inc.) were used to track individual bass while internal Passive Integrated Transponder (PIT) HDX12 PIT tags were used to identify individual juvenile salmon. Prior to tagging, salmon were anesthetized in a dose of MS-222 (0.2 g/L) buffered with $NaHCO_3$ (2 g/L) (Topic Popovic et al. 2012). All salmon were well below the 6.7% tag burden limit which may affect survival (Brown et al. 2010).

Enclosures

To measure salmon downstream travel speed, we built two rectangular floating field enclosures that were 9.1-m long, 0.9-m wide, and 0.6-m deep (Fig. 1). The frame was built of Polyvinyl chloride (PVC) pipe and enclosed with white 0.3 cm^2 mesh netting on all sides except for the top, which was covered with 2.5 cm^2 bird netting. The

downstream end also did not contain mesh and instead was covered with 3 cm^2 wire grid to allow salmon to exit into the river but prevent largemouth bass from escaping. The top PVC pipe was surrounded by pipe insulation, allowing the enclosures to float on the water surface with the long sides parallel to the shoreline. The enclosures were held in place by anchored buoys at two specific locations near the shoreline. We placed a PIT tag antenna around the outside of the enclosure frame one meter up from the downstream exit. Placement in front of the exit was to detect downstream movement before salmon may have started to exhibit caution due to approaching a novel environment (i.e. latency to exit). The enclosure design precluded some juvenile salmon natural antipredator behaviors, such as schooling and movements perpendicular to flow, but did allow predator inspection, vigilance, and cautious behavior, which are common fish antipredator behaviors over small spatial and temporal scales (Kelley and Magurran 2003).

Habitat structure

To test if structure modified salmon risk perception, we kept one enclosure empty and the other included habitat structure (Fig. 1). To imitate submerged aquatic vegetation, three plastic aquarium plants with three stems per plant (height: 0.27 m) were attached to the enclosure bottom at each of four equidistant points from the upstream to downstream length of the enclosure. To represent woody debris and overhanging vegetation, four 38-cm tall, 22-cm diameter cylinders of wire grid (2.5 cm^2) encased 5-10 sticks and were attached to the upper PVC frame and entered the enclosure from above. The four habitat cylinders were evenly distributed throughout the enclosure and alternated sides. We

rotated the enclosures with and without habitat structure between locations each week. Submerged aquatic plants and overhead sticks are the common forms of shoreline habitat structure in this study reach (M. Sabal pers. obs.).

Shade

To test if shade modified salmon antipredator decisions, we recorded if behavioral trials occurred in shade or direct sunlight. All trials occurred during daylight between 7:30 (90 mins after sunrise) and 19:00 (60 mins before sunset) on non-overcast days. Each enclosure location experienced different shade regimes from nearby trees on the levee casting shade onto one enclosure in the afternoon (after 16:00) and onto the other enclosure in the morning (before 11:00) (Fig. 2). Different shade regimes between the two locations helped disentangle the shade effect from time of day. The enclosures were visually broken up into five segments by structural PVC (Fig. 2). We noted how many sub-sections were more than 50% shaded and recorded these as the percent of enclosure shaded (possible values were 0, 20, 40, 60, 80, and 100%). To maintain sufficient sample sizes within shade categories for our analyses, we grouped the six percent shade categories into two categories: shade and sun. Trials were categorized as shaded when three or more sub-sections were shaded (60, 80, or 100% of the total enclosure), and trials were categorized as in sun when two or less sub-sections were shaded (0, 20, or 40% of the total enclosure).

Behavioral assay protocol

We ran behavioral assays, timing how long it took juvenile Chinook salmon to swim downstream through an enclosure with and without a largemouth bass. The difference in travel time between predator treatments represents salmon's behavioral reaction to predation risk. For predator trials, one largemouth bass was transported to the field enclosure and acclimated to the enclosure and river water for 30 minutes. For all trials, one juvenile salmon was transported to an acclimation container attached inside at the upstream end of the enclosure and acclimated to the river water for 10 minutes. To begin a trial, the container was opened and rotated to release the salmon into the enclosure, and this start time was recorded. The trial ended when the salmon reached the PIT tag antenna at the end of the enclosure or after one hour if never detected. Largemouth bass commonly swam throughout the enclosure, but we did not measure specific bass behavior. At the trial's end, we pulled a crowder through the enclosure to ensure the salmon exited and to recapture the largemouth bass. Only one salmon escaped the enclosure during a trial—all other salmon were accounted for at the end of the trial. An individual largemouth bass remained in the enclosure for two subsequent trials and then was removed. We rotated between two trials with a predator present and two trials with no predator, and we staggered which type of trial started in each enclosure. Each largemouth bass was only used once per week in two subsequent trials. We also staggered which enclosure started with hatchery or wild salmon and rotated every trial between each prey origin. All handling and procedures were approved under Institutional Animal Care and Use Committee (IACUC) protocol PALKE1701.

Analyses

To examine context-dependent salmon antipredator behavior in the migration corridor, we observed if travel speed was influenced by the interaction between predator presence and habitat structure, shade, and salmon origin. We used a mixed-effects Cox regression because it uses censored data over time—both measures of an event (salmon reaching the PIT antenna) happening or not (0,1) and the time at which that event occurred (R package: 'coxme'; Therneau 2015). Therefore, the Cox model response represents travel speed, as it measures the probability of reaching the antenna (traveling a set distance) over time and accounts for salmon that failed to reach the PIT antenna in the allotted 60 minutes. The preferred method is to include subjects with censored times in analyses because they represent important biological observations—the individuals with the most extreme behaviors (Fox 2015). Cox regressions appropriately consider those observations as censored and not as observations occurring at the cut-off time.

We included in the Cox model as main effects: predator presence (present, absent), structure (present, absent), shade (sun, shade), and salmon origin (hatchery, wild). We included all two-way interactions to assess how structure, shade, and salmon origin interact with predator presence and to account for other potential behavioral interactions among covariates. We included enclosure location as a random effect. We subsequently performed a Type III ANOVA on the Cox model to assess covariate significance. We used linear contrasts on the Cox model (R package: 'lsmeans'; Lenth and Love 2017) and effect sizes on log-transformed time to finish (Hedge's *g*; R package 'effsize'; Torchiano 2017) to determine post-hoc differences in reaction to predation risk among structure, shade, and salmon origin. Although unrelated to our specific hypotheses, we also tested if salmon traits (FL, weight, K condition factor) or

experimental attributes (time of day, date, days since salmon capture) affected the reaction of salmon to the predator. We used separate mixed-effects Cox models for each variable and related salmon travel speed to the interaction of predator presence and the variable of interest with location as a random effect, and subsequent Type III ANOVA tests.

Results

We performed 144 behavioral assays. The treatments we manipulated (predator presence, structure, and salmon origin) were approximately evenly distributed across total trials (after excluding overcast days). However, shade varied naturally, and treatments were uneven across shade and sun (Table 2). Water velocity inside the enclosure (mean + sd: 0.02 ± 0.01 m/s) was relatively low and consistent over the course of the experiments regardless of tidal stage. Hatchery and wild juvenile salmon varied over a similar size range (hatchery: 74 - 96 mm, wild: 72 - 109 mm FL). A summary of hatchery salmon physical attributes were (mean + sd: FL: 83.7 ± 4.6 mm, weight: 6.9 ± 1.2 g, K: 1.16 ± 0.06) and wild salmon attributes (FL: 80.8 ± 8.0 mm, weight: 7.6 ± 2.2 g, K: 1.02 ± 0.05). Neither salmon traits or experimental variables significantly influenced the reaction of salmon to the predator (Type III ANOVAs, N = 144: salmon FL [$\chi^2 = 0.90$, $p = 0.34$], salmon weight [$\chi^2 = 0.88$, $p = 0.35$], salmon K [$\chi^2 = 0.01$, $p = 0.90$], time of day [$\chi^2 = 0.39$, $p = 0.53$], date [$\chi^2 = 0.53$, $p = 0.47$], days since salmon capture [$\chi^2 = 0.92$, $p = 0.34$]).

Our enclosure design successfully measured salmon downstream travel speed. Most (131/144) salmon reached the PIT antenna at the end of the enclosure in the allotted

60 minutes, on average (± SD) in 8.5 ± 9.4 minutes with a distribution heavily skewed toward short times (Fig. 3). Salmon changed travel speed in response to predator presence and patterns were context dependent. Shade was the only covariate that significantly affected salmon's reaction to predation risk ($p = 0.002$; Table 1), and shade modified both the magnitude and direction of their antipredator response (Table 2; Fig. 4). As for magnitude, salmon reacted more strongly to the predator in shade (Linear contrast [predator vs. no predator]: predator present N = 20, predator absent N = 23, Z-ratio = 2.72, $p = 0.007$) compared to sun (predator present N = 48, predator absent N = 53, Z-ratio = -1.49, $p = 0.14$). As for direction, salmon slowed down in shade (statistically significant) and sped up in sun (non-statistically significant trend) (Fig. 4).

Because shade was the only significant variable that interacted with predator presence, we subsequently examined the effects of structure and salmon origin within shade and sun categories (Table 1). On average, structure dampened the reaction to the predator by 7.2 mins in shade (a difference between a large and small effect size) and increased the reaction by 3.6 min in sun (a difference between negligible and small effect size; Fig. 4B; Table 2). Also contrary to our expectations, hatchery and wild salmon reacted similarly to the largemouth bass—both groups slowed down in shade and sped up in sun (Table 2; Fig. 5). However, hatchery salmon slowed travel speed by 6.2 min more than wild salmon in shade with a larger effect size (Table 2).

Discussion

In this study, the presence of shade influenced salmon antipredator behavior in the migration corridor, more than habitat structure and salmon origin. Shade affected salmon

antipredator behavior in two ways. First, salmon reacted more strongly to the predator in shade than in direct sun. Second, shade affected salmon's escape tactic—when faced with the predator, salmon slowed down in shade and sped up in sun. These patterns were consistent across hatchery and wild salmon. Habitat structure did not significantly modify prey's perception of predation risk. These results suggest that environmental risk cues can affect both the magnitude and escape tactic of antipredator behavior, and in the migration corridor where prey have a propensity to travel directionally, these metrics can be observed via a change in travel speed with and without a predator present.

To examine context-dependent antipredator behavior in the migration corridor, we used large field mesocosms. Experiments are important to evaluate specific hypotheses, but difficult to perform on actively migrating animals (Marra et al. 2015). Experiments conducted on migratory prey in laboratory settings preclude a key component of migrant biology—the propensity to travel towards their destination (Able 1993; Pomeroy et al. 2006). We created large field enclosures that allowed salmon to travel downstream, while still allowing us to manipulate habitat and predator treatments to test our hypotheses. Despite their value in hypothesis-testing, experiments never fully capture the complete set of natural behaviors and processes. In our study, salmon could not use all possible antipredator behaviors, such as schooling, movements perpendicular to flow, or hiding in substrate (Steel et al. 2013; Furey et al. 2016). However, salmon were able to moderate activity levels, hide, and inspect the predator, which are all common antipredator responses in fish (Kelley and Magurran 2003). We did not anecdotally observe largemouth bass to actively pursue salmon, suggesting that our predators may not have exhibited threatening behavioral cues (Bateman and Fleming 2011). However,

largemouth bass are an important predator and plastic models have elicited behavioral responses in salmon (Sabal et al. 2020). Many laboratory assays use single cues or model predators, and by using a live predator, we ensured that realistic visual and olfactory predator cues were present (Reinhardt and Healey 1997; Lönnstedt and McCormick 2011). The experimental conditions (e.g., enclosure, handling) could have increased the perceived vulnerability of salmon over natural conditions affecting overall movement behavior, but were consistent across predator treatments, which is how we compared behavior to address our hypotheses.

In the migration corridor, juvenile salmon reacted the most strongly to the largemouth bass when in shade. The larger behavioral reaction suggests that salmon perceived shade to be a riskier environment than sun and could be driven by reduced visibility benefitting the predator in detection or capture (Cerri 1983; McMahon and Holanov 1995). Alternatively, salmon could have been compensating for low visibility reducing information by engaging in more antipredator behavior (Metcalfe 1984; Leahy et al. 2011). In our experiment, shade was created by trees on the leveed bank, which is similar to overhead or canopy shade rather than shade of in-water structure. Similarly, salmon avoid passing under anthropogenic structures because low light decreases prey vision and acquired information (Kemp et al. 2005; Leahy et al. 2011; Ono and Simenstad 2014). In our experiment, salmon had the largest reaction to the predator in shade with no structure (large effect size) and a smaller reaction in shade with structure (small effect size). This suggests a possible interaction between shade, structure, and predator presence, which deserves further study. In other circumstances when shade and structure are highly correlated, these conditions may indicate low risk. In upstream

habitats, rivers are small and bordered by riparian vegetation, so shade is often correlated with in-stream structure and typically indicates low risk (McMahon and Hartman 1989; Penaluna et al. 2015). Migrating salmon also preferentially hold in river reaches with complex habitat including shade with in-water structure (e.g. woody debris, submerged aquatic vegetation) (Zajanc et al. 2013).

Not only did shade affect the magnitude of the reaction to predation risk, but shade also affected what escape tactic juvenile salmon used. Cautious or cryptic antipredator behavior in migrating animals slows travel speed (Chung et al. 2009; Melnychuk and Welch 2018), while fleeing past predators causes prey to speed up (Peterson 1976; Proffitt et al. 2009). In our study, juvenile salmon slowed down in shade and sped up in direct sun in response to the predator. In the shade salmon may have used cautious or cryptic antipredator behavior, such as predator inspection, reduced movement, and hiding (Kelley and Magurran 2003). These behaviors may be advantageous in shade because low light decreases the detection distance between predator and prey, thereby allowing salmon to be cryptic before they are first detected by the predator (Howick et al. 1983; Mazur and Beauchamp 2003).

In contrast, salmon may have been immediately detected by the largemouth bass in direct sunlight, thereby reducing the success of slowing down to be cryptic. When in sun salmon exhibited a trend to speed up in response to the predator (although not statistically significant). The weaker reaction and larger behavioral variation to predation risk in sun suggests that salmon may have perceived the sun-lit environment as relatively low risk. Sunlight allows prey to gather information and characteristics such as predator gaze, orientation, and approach speed, which indicate the likelihood and severity of a

predator attack (Cooper 2008; Bateman and Fleming 2011). The largemouth bass in our experiment actively swam up and down the enclosure, but we never anecdotally observed them actively pursue a salmon. Perhaps salmon in direct sunlight could determine that the predator was not a major threat in that moment, and therefore, salmon did not significantly alter their behavior. Our study precludes examination of salmon responses to partial shade because we considered percent shade as a binary category (shade, sun) to ensure sufficient sample sizes across treatments. Therefore, we may have missed biologically-relevant nuances between predator and prey along the partial shade gradient and related to the location of predator and prey relative to shade and sun (McCartt et al. 1997). In our study, salmon shifted escape tactics between shade and sun related to predator presence.

Shade affected the magnitude and direction of the reaction to a predator, and both patterns were consistent across hatchery and wild salmon. Hatchery salmon often fail to appropriately react to predators (Leduc et al. 2007; Jackson et al. 2011; Solberg et al. 2020). Therefore, we predicted that hatchery salmon would react less than wild salmon to predator presence due to their lack of prior predator exposure. Contrary to our expectations, hatchery salmon reacted similarly to wild salmon and reacted more strongly to the predator in shade. There is some evidence for innate antipredator responses to predator odor cues in juvenile salmon and responses to shade in hatchery bluegills (*Lepomis macrochirus*) (McCartt et al. 1997; Hawkins et al. 2007, 2008). Hatchery salmon may have innately responded to risk cues in our experiment. Wild salmon associate predator encounters with many cues including predator characteristics and habitat associations. In our experiment, wild salmon may have been better at accurately

assessing local predation risk and could tell the predator was not actively foraging. This information could have allowed salmon to take advantage of the tradeoff between predation risk and other activities by avoiding behavioral changes more than necessary. The consistent patterns in antipredator behavior and shade across hatchery and wild salmon emphasize the importance of shade to modifying predation risk.

We were surprised that shade was more important and consistent in affecting salmon antipredator responses over habitat structure. Structure strongly and regularly decreases predation risk to diverse prey (Crowder and Cooper 1982; Anibal Stellatelli et al. 2015; Bonnot et al. 2016). However, resident prey are familiar with their surrounding environments, while migrating prey travel though relatively unfamiliar migration corridors (especially first time migrants). Perhaps, in the migration corridor, unfamiliar structure is less certain whether it indicates low or high risk compared to shade. In familiar environments, the pattern is often opposite—structural cues of low risk elicit stronger antipredator responses over visibility-related risk cues (Diehl 1988; Ajemian et al. 2015). However, structure indicating low risk depends strongly on specific knowledge of refuge location and safety. For example, eastern chipmunks (*Tamias striatus*) quickly retreat to burrows in familiar environments, but in unfamiliar environments, they do not know the location of burrows and instead take longer to run up trees (Clarke et al. 1993). Shade may consistently affect visibility, and, therefore, be less affected by local knowledge. For migrating prey, unfamiliar environments could change the relative importance among different risk cues and this idea deserves further study (Németh and Moore 2007; Bazazi et al. 2011; Sabal et al. 2021).

Our study suggests that shade is important in modifying the magnitude and tactics of antipredator behavior for juvenile salmon in the migration corridor. Furthermore, because antipredator behaviors in the migration corridor relate to travel speed, there is potential for these fine-scale decisions to scale up and affect larger patterns in migratory behavior. For example, decisions to temporarily hide or move nocturnally can delay arrival to the migration destination (Melnychuk and Welch 2018). Conversely, decisions to speed up to reduce predator encounters can shorten migration duration or cause early arrival (Hebblewhite and Merrill 2007). As optimal arrival time is often narrow for migratory prey, delays or advances to arrival timing may have important population consequences (Gienapp and Bregnballe 2012). Therefore, fine-scale decisions in the migration corridor, how they relate to movement, and how they may scale up to migratory patterns are valuable future research directions. Overall, this study expands our knowledge about antipredator behavior in the migration corridor by showing how environmental risk cues can shape the magnitude and tactics of how migrants react to predation risk and how these responses relate to movement.

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Conflict of Interest: The authors declare that they have no conflict of interest.

Ethical approval: All applicable institutional and/or national guidelines for the care and use of animals were followed.

Author Contributions: MCS, EPP, and JEM conceived and designed the experiments. MLW coordinated field work for obtaining study organisms and MCS ran the experiment and performed the analyses. MCS wrote the first draft of the manuscript and all authors contributed substantially to revisions.

Table 2.1 Results of Type III ANOVA on mixed-effects Cox regression

Covariate	**df**	χ^2	**p**
Predator	1	7.58	0.006*
Shade	1	15.16	< 0.001*
Structure	1	4.86	0.03*
Origin	1	2.42	0.12
Predator x Shade	1	9.25	0.002*
Predator x Structure	1	2.04	0.15
Predator x Origin	1	0.39	0.53
Shade x Structure	1	3.73	0.05†
Shade x Origin	1	5.56	0.02*
Origin x Structure	1	< 0.001	0.99

† $p < 0.1$, * $p < 0.05$

Table 2.2 Summary of pair-wise linear contrasts and effect sizes. Describes how, for various habitat and salmon origin treatments, predator presence changes salmon speed. N represents the number of trials. All predator present and absent trials of first four rows equal 144 total trials, and likewise for the last four rows

Treatment	Predator contrast		Linear contrast		Effect size	
	Predator present (N)	Predator absent (N)	Z-Ratio	p	Hedge's *g*	Magnitude˚
Shade – no structure	10	5	2.80	0.005*	1.07	large
Shade – structure	13	15	1.97	0.048*	0.42	small
Sun – no structure	27	31	-0.20	0.85	-0.09	negligible
Sun – structure	21	22	-1.94	0.053†	-0.21	small
Shade – hatchery	10	9	2.65	0.008*	1.01	large
Shade – wild	13	11	2.24	0.03*	0.20	negligible
Sun – hatchery	25	27	-0.75	0.45	-0.08	negligible
Sun – wild	23	26	-1.55	0.12	-0.20	negligible

˚Magnitude of effects interpreted following the thresholds $|g| < 0.2$ "negligible", $|g| < 0.5$ "small", $|g| < 0.8$ "medium", $|g| > 0.8$ "large" (Cohen 1992).

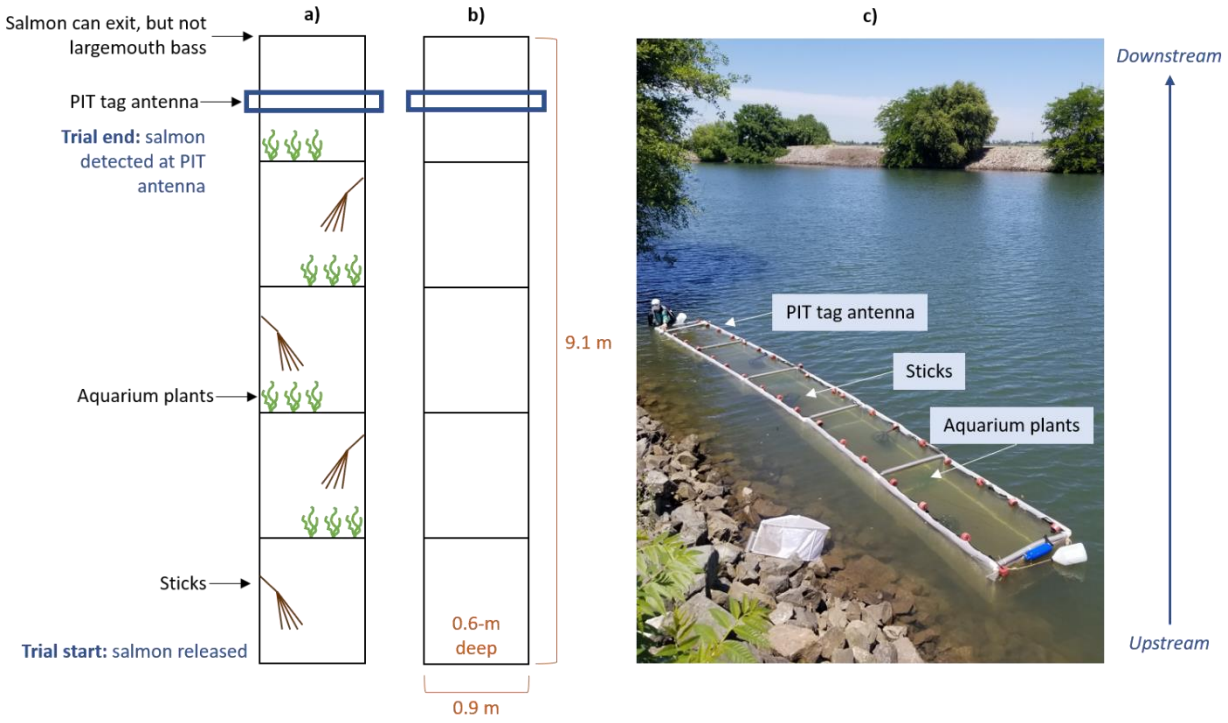

Figure 2.1 Diagram of enclosure set up, a) enclosure with structure, b) enclosure without structure, c) photograph of enclosure with structure in sun

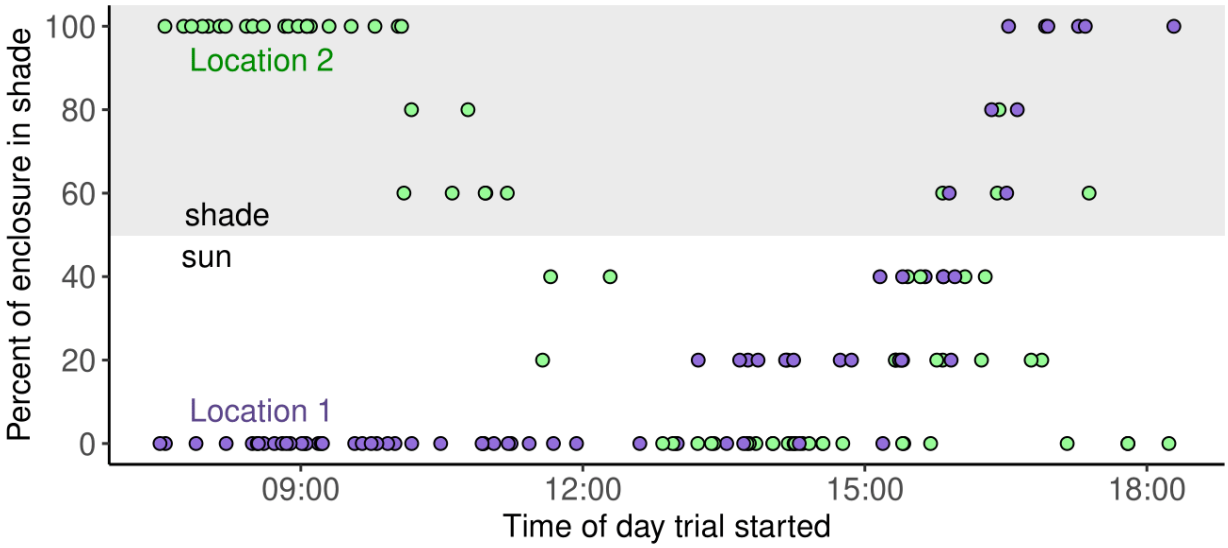

Figure 2.2 Shade and sun regimes over time of day at each enclosure location: location 1 (purple) and location 2: (green). Shade trials occurred when the enclosure was 60, 80, or 100% in shade, while sun trials were when the enclosure was 0, 20, or 40% in shade

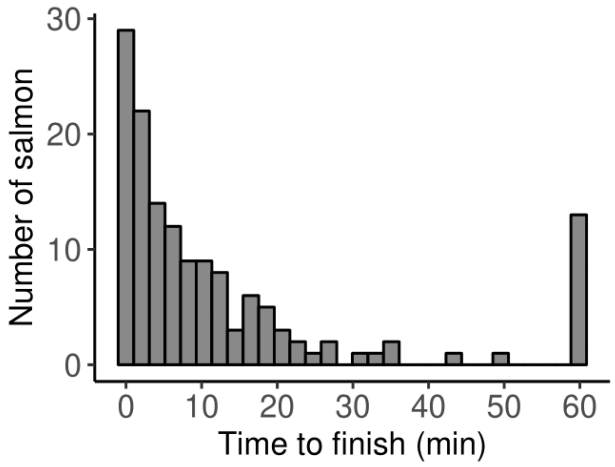

Figure 2.3 Histogram of time to reach the end of the enclosure (min) across all salmon (*Oncorhynchus tshawytscha*) trials. Salmon binned at 60 min did not finish in the allotted 60 min. Salmon with censored times were not considered as 60 mins in analyses, but instead were appropriately included in Cox regressions as censored values

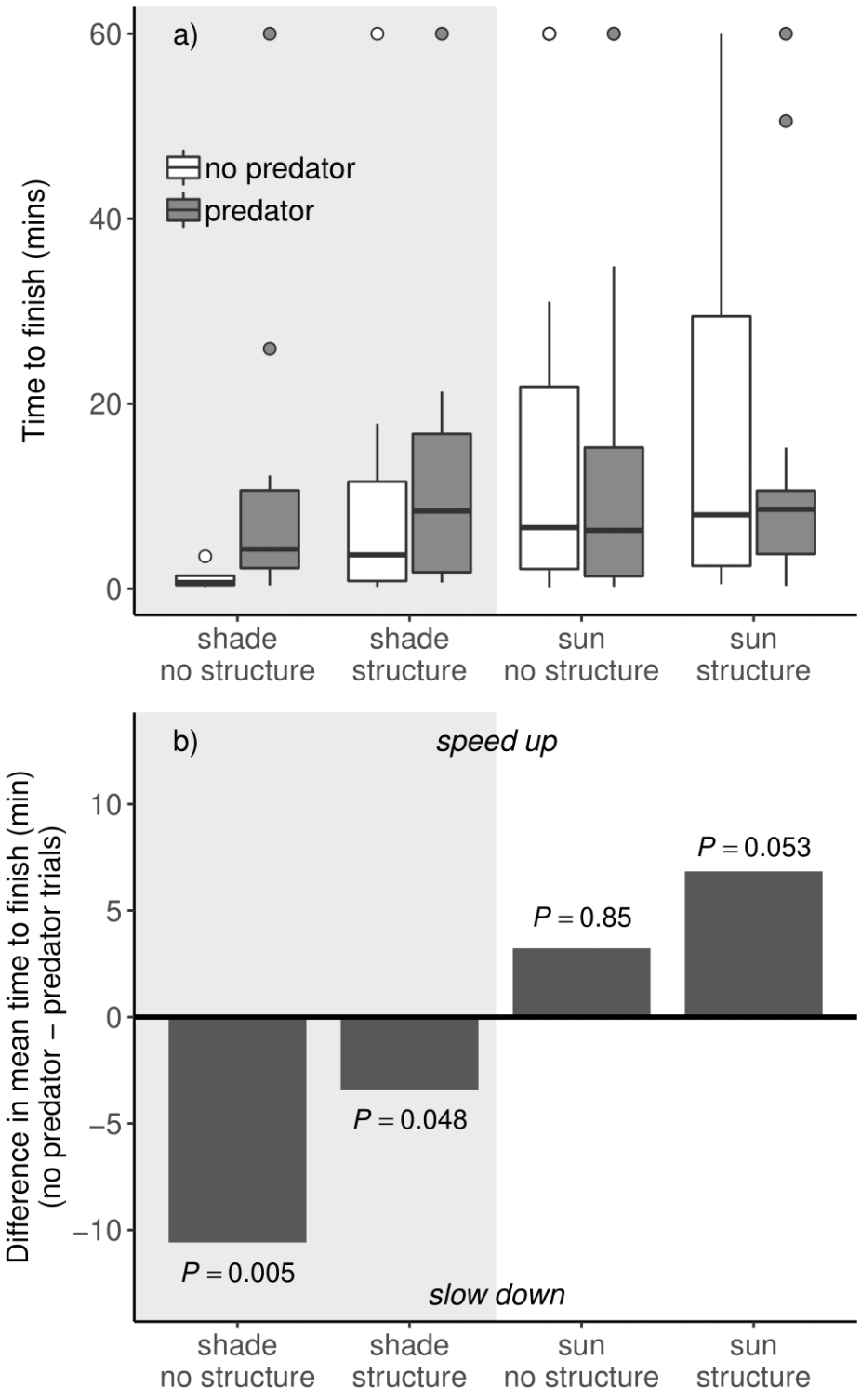

Figure 2.4 a) Boxplot of salmon's time to finish (min) for each habitat treatment combination of shade and structure, by predator treatment (gray = predator, white = none). Whiskers represent 95% confidence intervals. b) Bars represent the difference in the mean time to finish (min) between no predator and predator trials of each habitat

treatment. Positive values indicate the salmon sped up, while negative values indicate the salmon slowed down, on average when the predator was in the enclosure. P-values relate to the contrast between predator and no predator trials within habitat categories (Table 2)

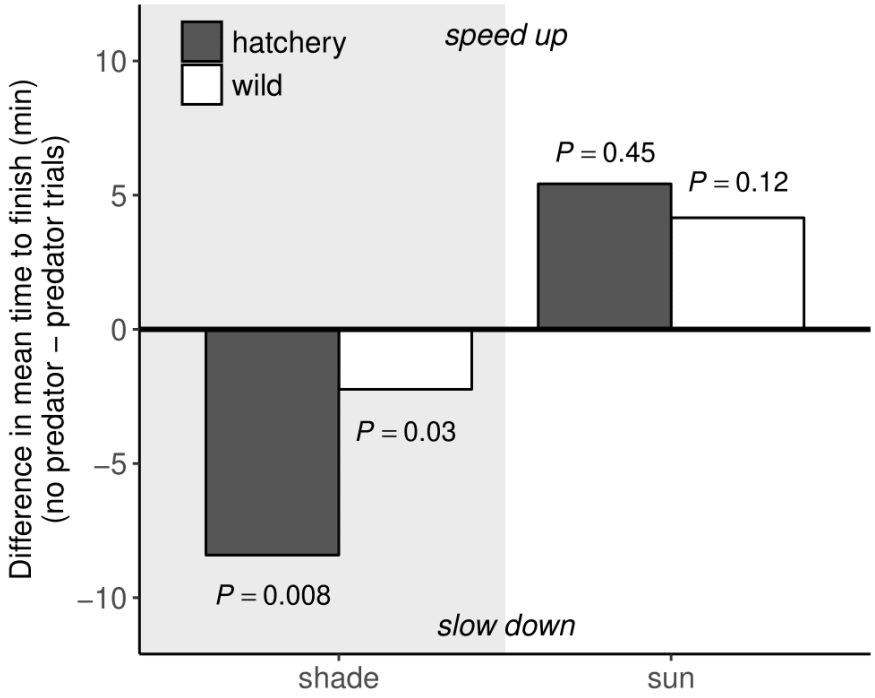

Figure 2.5 Bars represent the difference in the mean time to finish (min) between no predator and predator trials in the shade and sun. Dark bars represent hatchery salmon while white bars represent wild salmon mean behavior. Positive values indicate the salmon sped up, while negative values indicate the salmon slowed down, on average when the predator was in the enclosure. P-values relate to the contrast between predator and no predator trials within shade and salmon origin categories (Table 2

Chapter 3: Predation landscapes influence migratory prey ecology and evolution

Keywords: migration, predation risk, antipredator behavior, anthropogenic change

Abstract

Migratory prey experience spatially-variable predation across their life cycle. They face unique challenges in navigating this predation landscape, which affects their perception of risk, antipredator responses, and resulting mortality. Variable and unfamiliar predator cues during migration can limit accurate perception of risk, and migrants often rely on social information and learning to compensate. The energetic demands of migration constrain antipredator responses often through context-dependent patterns. While migration can increase mortality, migrants employ diverse strategies to balance risks and rewards, including life history and antipredator responses. Humans interact frequently with migratory prey across space and alter both mortality risk and antipredator responses, which can scale up to affect migratory populations and should be considered in conservation and management.

Predators and Migratory Prey

Animal **migrations** (see Glossary) are spectacular phenomena where concentrated and conspicuous animal movements often result in striking predator-prey interactions across the migratory life cycle (Figure 1). Predators influence prey ecology and evolution through an integrated process of **mortality risk,** set by

predator communities and habitats, followed by prey **perception** of risk, which informs their **antipredator responses**, which further reduce mortality all balanced by the underlying tradeoff between risk and reward (Creel et al. 2019; Gaynor et al. 2019). While this process applies broadly across prey species, migratory prey face unique challenges at each of these stages. First, mortality risk can be high and spatially variable because migratory prey are aggregated, predictable in their distributions, and willing to take on high risk in some locations to reap the benefits of **fitness rewards** in others. Second, **predator cues** can be highly variable and locally unfamiliar to migrants traveling across vast geographic space (Moore 2018). Third, antipredator responses require energy, while migration is already energetically demanding (Klaassen et al. 2012). Finally, humans interact frequently with migrants across space and political boundaries and can modify predator-prey interactions at each stage with consequences for migratory populations.

These challenges for migrants related to mortality risk, perception, and antipredator responses can result in diverse ecological and evolutionary outcomes, which can further be connected across space and time (Gaynor et al. 2019). Tradeoffs among time, energy, and predation shape migration life histories, but diverse outcomes related to these unique predation challenges and connections have been less explored (Alerstam 2011). Recently, there is an emerging interest in the influence of species interactions on migration, including migratory coupling, co-migration, and disease (Altizer et al. 2011; Bauer and Hoye 2014; Kays et al. 2015; Furey et al. 2018; Cohen and Satterfield 2020). Existing frameworks of theoretical landscapes

conceptualize spatially varying consequences of predation on their prey (e.g., landscapes of fear, disgust), but do not specifically consider the additional spatial variation and ecological and evolutionary consequences from a migratory life history (Gallagher et al. 2017; Weinstein et al. 2018). We extend **predation landscapes** as a framework to conceptualize the variability of predator effects across the migratory life cycle separated into related components of mortality risk and antipredator responses. Using this framework, we ask: (1) how do the unique challenges migratory prey face related to predation affect mortality risk and antipredator responses across the migratory life cycle?; (2) how have humans altered predation landscapes with consequences for migratory prey?; and (3) how can we restore these landscapes to conserve migratory populations?

Predation Landscapes for Migratory Prey

Geographic variation in predator communities and habitat features lays the foundation of mortality risk (sometimes called "danger"), which is conveyed to migratory prey through predator cues, allowing an antipredator response, which further lowers resulting mortality risk (Creel et al. 2019; Gaynor et al. 2019). We consider a predation landscape as the two measurable components of this integrated process: spatially-variable mortality risk after the modifying influence of responses (**risk landscape**) and migratory prey antipredator responses (**response landscape**) (Figure 2) (Gallagher et al. 2017; Weinstein et al. 2018). As in the original landscape of fear, prey responses are often assumed to correspond with mortality based on

prey's accurate perception of risk, which can result in the evolution of diverse prey responses (Figure 2A) (Laundre et al. 2010). However, recent research highlights that ecological constraints and tradeoffs, which may be particularly pressing in a migratory life history, often cause spatially concurrent risk and response landscapes to vary in topography (i.e., magnitude of peaks and valleys), thus it is important to consider both landscapes as distinct (Bleicher 2017; Gaynor et al. 2019). An appropriate antipredator response can effectively minimize mortality risk while balancing the costs of behavior (Figure 2B), while unfamiliar predator cues can constrain perception and reduce antipredator responses despite high mortality. Migratory prey may prioritize energy for migration fueling or traveling instead of antipredator responses despite risk (Figure 2C). Humans can also alter the magnitude or distribution of risk too quickly for natural selection to favor adaptive responses (Figure 2D) (Carthey and Blumstein 2018). This predation landscape framework conceptualizes spatially varying predator effects across the migratory life cycle, which occur as mortality risk and antipredator responses, and highlights relationships among risk and responses as influenced by unique migratory challenges.

Risk Landscape

Mortality risk varies across the migratory life cycle due to variation in predator communities and habitat features. Migrants often experience high mortality in the **migration corridor** from conspicuous migratory movements and groups and an obligation to traverse exposed habitats (Hebblewhite and Merrill 2007; Friedman

et al. 2019). Predator behavior also contributes to spatial patterns of risk. Predators may track migrants along the corridor, as when wolves (*Canis lupus*) follow migrating caribou (*Rangifer tarandus*) or when free-tailed bats (*Tadarida brasiliensis*) track migratory insects (McCracken et al. 2012; Furey et al. 2018; Joly et al. 2019; Cohen and Satterfield 2020). Spatially-distinct peaks of risk can also occur when predators aggregate and intercept migrants at migratory pinch points (Furey et al. 2018). For example, bears (*Ursus* spp.) show a numerical response in abundance and consume large proportions of adult salmon (*Oncorhynchus* spp.) in shallow, narrow streams (Quinn et al. 2017). Spatial variation in predator abundance also creates variable mortality risk, such as when predators of migrant birds are constrained to stopover site habitats (McCabe and Olsen 2015).

Migratory prey may tolerate high mortality risk at **migratory destinations** if they are outweighed by fitness benefits of migration, such as increased reproduction or survival at other life stages. In summer, adfluvial roach (*Rutilus rutilus*) occupy lakes where there are many foraging opportunities despite high mortality. In winter, they migrate to safer streams with lower food when lake food declines and predatory birds arrive – shifting the ratio of risk to reward (Figure 2A) (Skov et al. 2013; Hulthén et al. 2015). The risk landscape represents the resulting probability of mortality and, therefore, is not only driven by extrinsic properties of predator communities and habitat but is also a function of the success of antipredator responses. For example, an area with abundant predators will have low mortality on our risk landscape if prey can behaviorally avoid predation. Therefore, to fully

understand the risk landscape we must also consider the processes that drive and challenges that constrain antipredator responses, which starts with perception of risk.

Perception of Risk

Migrating prey encounter varied and unfamiliar predator cues, challenging accurate perception of risk. As migrants travel along the migration corridor, they continuously encounter unfamiliar environments (Németh and Moore 2014; Moore 2018). Even if migrants know the area from prior migrations, they have less information about local risk than animals living in a well-known home range (Yoder et al. 2004). Furthermore, environmental risk cues likely vary in meaning (risk vs. safety) or reliability across the heterogeneous migratory landscape. To compensate for less reliable predator cues, migrants may rely on social information, which can be obtained quickly with relatively low cost (Németh and Moore 2007). With less direct information about predators, migratory birds often use density of conspecifics at stopover sites to determine where to forage safely and efficiently (Németh and Moore 2014). Additionally, many migrants travel in groups, and collective decisions are critical to navigation, movement, and predator evasion across ungulates, birds, fish, and insects (Ren et al. 2016; Rieucau et al. 2016; Fryxell and Berdahl 2018; Storms et al. 2019). Sometimes experienced individuals or "leaders" can disproportionately detect and process information for the migratory group (Guttal and Couzin 2011; McComb et al. 2011). Although migratory animals use diverse predator cues (visual, chemical, auditory, habitat), which relate to taxa-specific physiology, social

information may be particularly valuable to migrants across taxa to inform them of mortality risk in variable environments.

Once perceived, information must be cognitively processed to elicit an appropriate antipredator response. Learning allows migrants to accurately perceive risk despite variable and unfamiliar environments. In a field experiment, adult Atlantic salmon (*Salmo salar*) learned to avoid fishing gear over the course of their upstream migration where humans are acting as a predator (Lennox et al. 2016). Migratory elephants (*Loxodonta africana*) learned with age to more accurately process the meaning of experimental playbacks of roaring male lions (*Panthera leo*), making losses of old individuals to poaching especially harmful to the group's success (McComb et al. 2011). For both cases, learning improved antipredator responses. Migrants may use social information and learning to overcome the challenges of variable and unfamiliar environments to perceive information about risk and connect cues to appropriate antipredator responses.

Response Landscape

Prey decide how to respond to risk cues based on individual traits affecting vulnerability and other demands requiring energy. Energetic demands of migration can compete with costs of antipredator behavior. For migrants, costs of antipredator behavior can include immediate energetic costs from engaging in an antipredator response (e.g., flight) or immediate opportunity costs from spending time avoiding predators instead of other activities that benefit fitness (e.g., refueling, traveling,

navigating). Future opportunity costs also exist because antipredator responses can affect movement and migration timing (e.g., departure, arrival) and deviations can be costly as optimal migration timing can be narrow (e.g., synchronized with resource pulses at migratory destinations or in corridors) (Houston 1998; Aikens et al. 2017; Sabal et al. 2020). Therefore, the energetic demands of migration may constrain antipredator responses during preparation or active migration, despite mortality risk (Hopcraft et al. 2014; McCabe and Olsen 2015). For example, long-distance avian migrants were more constrained by time and thus prioritized stopover sites based on food quality and ignored mortality risk, while short-distance migrants selected stopover sites based on a balance between foraging and habitat refuge (Figure 2C) (McCabe and Olsen 2015). In the wet season, migrating zebra (*Equus burchelli*) slowed down and changed course to avoid woodlands that provide cover to ambush predators. However, in the dry season when the costs of antipredator behavior are greater due to fewer foraging opportunities, zebra migrated directly through woodlands to save energy despite added mortality risk (Hopcraft et al. 2014).

Despite the energetic costs of migration, we still observe diverse antipredator responses that reduce mortality risk in migratory prey and vary across the landscape. In corridors, migrants can reduce risk by using routes that avoid predators. Killer whales (*Orcinus orca*) hunt bowhead whales (*Balaena mysticetus*), but bowhead whales rarely fall prey to killer whales when they migrate close to coastal sea ice refugia (Figure 2B) (Matthews et al. 2020). Predation landscapes not only vary in space, but also in time. Nocturnal migration is a widespread phenomenon (e.g.,

insects, fish, birds) that allows prey to move at times when visual predators cannot effectively hunt (Chapman et al. 2015; Furey et al. 2016; Komal et al. 2017). Over decades of observational studies, migrating adult western sandpipers (*Calidris mauri*) increased migration speed to stay ahead of and temporally avoid overlap with the approaching peak abundance of migrating peregrine falcons (*Falco peregrinus*) (Hope et al. 2014). At destinations, migratory prey can minimize risk by departing earlier or arriving later to limit exposure to predators (Hulthén et al. 2015; Harts et al. 2016). When mortality risk cannot be spatially or temporally avoided, other antipredator responses, such as increasing vigilance, using habitat refugia, and traveling in groups, can still lower mortality during migration (Hopcraft et al. 2014; McCabe and Olsen 2015; Furey et al. 2016; Santos et al. 2016).

Ecological and Evolutionary Consequences

The unique migratory challenges related to mortality risk, perception, and antipredator responses each vary across the migratory life cycle, which drives ecological consequences connected across space and time depending on where responses and risk occur (Marra et al. 2015). Antipredator responses in the migration corridor can alter arrival timing, which may affect growth, survival, or reproductive success at destinations (Jonker et al. 2010; Sabal et al. 2020). Mortality in risky corridors can affect population demography (Friedman et al. 2019). High rates of predation in one geographic location may also benefit migratory populations in later life stages through compensatory mechanisms including releasing survivors from

competition or removing infected or low-condition individuals from the population (Miller et al. 2014; Tucker et al. 2016; Furey et al. 2021). Changing risk at destinations can shift tradeoffs and affect the propensity or timing of migration (Jonker et al. 2010; Hebblewhite and Merrill 2011). Migrants may also transfer predator effects across space to different communities and ecosystems. When predators cause migratory prey to shift distributions or routes, there can be subsequent ecological consequences for lower trophic levels spread across the migratory route (Orrock et al. 2010; Boyce 2018) (Box 1). By predators both consuming prey and causing prey to change behavior, predators can modify the number and size of migrants moving among distant ecosystems, thereby altering the flow of energy and nutrients across ecosystem boundaries (Box 2).

A shared evolutionary history over long timeframes between migratory prey and their risk landscape results in diverse mechanisms of perception and patterns of responses. Behavioral traits, such as arrival time, group synchrony, and nocturnal migration are evolved migratory strategies, which can reduce mortality risk (Furey et al. 2016; Harts et al. 2016). Predation pressure, in combination with other factors, may contribute to the evolution of a migratory life history strategy (Houston 1998; Alerstam 2011). Diel vertical migration, altitudinal migration, partial migration, and seasonal migration have evolved, in some instances, to reduce mortality risk balanced by fitness rewards (McKinnon et al. 2010; Skov et al. 2013; Dawidowicz and Pijanowska 2018; Lundblad and Conway 2020). Migratory prey often have frequent interactions with humans across ecosystems and political boundaries, which can alter

predators, prey, and the environment. Humans, thereby, modify both risk and response landscapes on short timeframes, disrupting their evolutionary balance with myriad consequences for migratory prey.

Humans Change the Risk Landscape

Humans alter predator populations and can broadly shift the magnitude of mortality risk across the landscape (Fleming and Bateman 2018). Humans introduce nonnative predators, which increases risk in new spatial patterns. Climate change also affects predator distributions and risk. Warming spring temperatures caused elderberry (*Scambucus racemosa*) to flower early and drew brown bears (*U. arctos*) away from migratory salmon (*O. nerka*) streams (Deacy et al. 2017). Native top predators, including marine mammals, birds, and carnivores, often consume and rely on migratory prey, and humans have broadly modified mortality risk through predator exploitation and subsequent recovery with diverse ecological effects. For example, after exploitation was halted, pinnipeds recovered and increased consumption of Chinook salmon (*O. tshawytscha*) (Chasco et al. 2017). Peregrine falcon recovery in the wake of a DDT ban caused migrating semipalmated (*Calidris pusilla*) sandpipers to shift to safer migratory routes (Hope et al. 2020). Gray wolf recovery induced antipredator responses of migratory elk with cascading consequences for ecosystems (Box 1) (Boyce 2018). Finally, humans can decrease the condition of migratory prey, rendering them more susceptible to predation (e.g., disease from aquaculture, stress from fisheries handling, and reduced foraging habitat quality) or decrease prey

abundance, indirectly reducing the effectiveness of safety in numbers (Klaassen et al. 2012; Raby et al. 2014; Peacock et al. 2015; Furey et al. 2016).

On finer scales, humans also modify the topography of the risk landscape. Humans can attract predators unevenly across the migratory landscape, such as humans introducing domestic cats (*Felis catus*) that prey on migratory birds following human populations (Mcruer et al. 2017). This variation in risk across the migratory life cycle may affect antipredator responses and survival, which can furthermore influence migration patterns and demography. Alternatively, predator avoidance of human activity can create local safe refuges. A portion of the Ya Ha Tinda elk (*Cervus elaphus*) population migrates to summer ranges to, in part, avoid higher wolf densities at lower elevations. However, because wolves avoid humans, resident elk reduce risk by selecting refugia near humans, shifting the risk-reward balance between resident and migratory life histories (Hebblewhite and Merrill 2011). Humans can also create beneficial predator hunting habitat. For example, anthropogenic linear features (e.g., pipelines, roads) increase carnivore hunting efficiency on migratory ungulates and dams increase avian and piscivore feeding on outmigrating juvenile fish (Figure 2D) (Evans et al. 2016; Sabal et al. 2016; Boulêtreau et al. 2020; Dickie et al. 2020).

Humans Change the Response Landscape

Human activities can modify the ability of migratory prey to detect and process cues, thereby altering the response landscape. Noise and light pollution can

be major challenges for migratory prey as they frequently travel through human-modified landscapes (Dominoni et al. 2020). When migratory songbirds arrived at stopover habitats near simulated traffic noise, some species avoided noisy areas altogether presumably because noise impeded their ability to detect predators and therefore increased mortality risk. Other species remained but increased vigilance to compensate for noise disrupting auditory predator cues and suffered reduced body condition – a cost of antipredator behavior (Ware et al. 2015). As a misleading cue, naval sonar elicited an antipredator response in beaked whales (*Mesoplodon densirostris*) comparable to predatory killer whale vocalizations, imposing a defensive cost that did not match actual risk (Tyack et al. 2011). Migratory prey often use light for navigation and artificial light can attract birds and insects, increasing mortality by benefiting visual predators (Owens et al. 2020). Artificial light from skyscrapers attracted migrating songbirds which were consumed by predatory falcons using the structure as ambush habitat (DeCandido and Allen 2006; Cabrera-Cruz et al. 2018). Light indicates risk for zooplankton as it increases vulnerability to visual predators; therefore, light pollution can also signal zooplankton to stay in deeper water at night, disrupting natural migratory patterns (Ludvigsen et al. 2018).

Humans also can impede learning in migratory prey, which reduces the cognitive ability to respond appropriately to mortality risk. Some migratory populations are supplemented by captive breeding programs (e.g., fish, birds, ungulates), which reduce learning opportunities about predation and can result in captive-bred individuals exhibiting low antipredator responses and experiencing high

mortality (Imlay et al. 2010; Jesmer et al. 2018; Solberg et al. 2020). Migratory population declines may also reduce social information quantity, while removal of knowledgeable individuals (e.g., elephant matriarchs) may reduce information quality – both potentially reducing migratory prey cognitive processing about risk (McComb et al. 2011). Pollutants, noise, and light can also distract prey, which can interfere with cognitive processing including spatial awareness and memory, and these concepts should be further investigated in how migratory prey interact with predators (Dominoni et al. 2020; Jacquin et al. 2020). Ecological-evolutionary mechanisms, including the timescale of evolutionary history between risk and responses, may contribute to either appropriate or inappropriate antipredator responses in migratory prey (Carthey and Blumstein 2018; Watts and Truitt 2021).

Restoring Predation Landscapes

To restore healthy predation landscapes for migratory prey, the most sustainable and effective conservation strategies involve habitat restoration because altered habitats are often the ultimate cause of changes that either favor or harm natural predator populations and alter prey vulnerability (Spangenberg et al. 2019; Cohen and Satterfield 2020). Protecting key habitats along common migratory routes (e.g., flyways, swimways) can benefit populations of co-migrating predators and prey through increased abundances and more naturally dispersed distributions (Cohen and Satterfield 2020). When permanently protecting large areas of migratory corridors is not feasible, dynamic protected areas that use near-real-time migrant location

information can protect critical habitats only during times of high migrant use (Bauer et al. 2016; Oestreich et al. 2020). Increased connectivity, through tunnels, overpasses or tree patches within an open landscape, can also allow migrants to move with more protection and exhibit more risk-averse behavior (Silva et al. 2020). Removing anthropogenic features that inflate predation success may also reduce mortality on migrants, such as when eastern snapping turtles (*Chelydra serpentina*) ambush migrating river herring (*Alosa* spp.) at culverts (Alcott et al. 2020). Habitat restoration can also provide refugia, which allows prey to utilize certain antipredator responses. For example, restored deep stream pools for rearing salmon and artificial ponds for breeding piping plovers (*Charadrius melodus*) benefited migratory prey because nearby refugia allowed them to exploit favorable foraging-risk tradeoffs increasing their energy gain (Maslo et al. 2012; Polivka 2020). Additionally, juvenile Chinook salmon preferred to temporarily pause their outmigration at natural and restored shoreline habitats compared to rock-covered leveed banks presumably because of increased protection from predators (Hellmair et al. 2018).

Additional conservation tools include directly modifying predator abundance or prey vulnerability. Tightened harvest regulations, such as the Marine Mammal Protection Act of 1972, can protect and promote recovery of native top predators that rely on migratory prey (Chasco et al. 2017). Relaxed regulations and targeted removals are sometimes attempted to decrease predator populations (Sabal et al. 2016; Marolla et al. 2019). However, native predators are integral to healthy ecosystems and their removal should be avoided whenever possible. For native and

nonnative predators alike, removals are often ineffective due to compensatory mortality and complex food web interactions (Doherty and Ritchie 2016; Lennox et al. 2018). Creating artificial refuges provides an alternative to removing predators. Maternity penning of ungulates on breeding grounds, nest exclosures for breeding birds, and captive-rearing and translocating migratory juvenile fish protect migratory prey during vulnerable life stages (Holsman et al. 2012; Cohen et al. 2016; Serrouya et al. 2019). However, these strategies have their own downsides, such as captivity impeding future antipredator behavior, and are best used as a temporary strategy to protect migratory prey when populations are very low (Doherty and Ritchie 2016).

Conservation approaches are also emerging that manipulate antipredator responses via perception to match human-inflated mortality risk (Fleming and Bateman 2018; Dominoni et al. 2020). These approaches may be useful when there are obstacles to restoring habitats or as alternatives to modifying predator populations. For example, predator conditioning in fish hatcheries by adding alarm cues has increased hatchery-reared fish antipredator responses (Horn et al. 2019). To attract migratory grasshopper sparrows (*Ammodramus savannarum*) to newly restored habitats, broadcasting conspecific vocalizations (i.e., adding social information) nearly doubled sparrow abundances, and this approach could be used to signal safe stopover sites (Andrews et al. 2015). Sea lamprey (*Petromyzon marinus*) migrating upstream avoid routes with conspecific alarm cues, and in their nonnative range in the Great Lakes these alarm cues can be manipulated to ‘push’ lamprey towards traps for removal (Box 3) (Hume et al. 2020).

Concluding Remarks

Migratory prey face unique challenges related to predation presenting ecological constraints and tradeoffs that result in diverse ecological and evolutionary outcomes. To overcome the challenges of responding appropriately to variable and unfamiliar predator cues, migratory prey across taxa utilize social information and learning. The required cognitive mechanisms, the sources of information they use, and the relative importance among cues remain key areas for future research (see Outstanding Questions). The energetic demands of migration constrain antipredator behavior and patterns of such behavior are often context dependent. Additionally, some migratory prey exhibit antipredator responses that effectively keep mortality risk low, while others are vulnerable and experience high and variable mortality across the landscape. Risk and response landscapes represent distinct outcomes of predation and pathways to affect populations, communities, and ecosystems connected across space and time.

Consequences of human-altered predation landscapes can be easily missed in migratory prey because causes and effects may be separated across space and time and outcomes may appear as antipredator responses or mortality risk. Therefore, human impacts on migratory prey populations through altering predator-prey interactions are underappreciated and often ignored in conservation and management. Rapid anthropogenic change creates evolutionary mismatches within the predation process, which can exacerbate mortality or elicit unnecessary and costly antipredator

responses. An additional obstacle is that conservation approaches for migratory prey may require coordination across political boundaries. Despite these challenges, prioritizing habitat restoration to regain healthy predator-prey balance mixed with diverse approaches that target both the risk and response landscapes has potential to restore predation landscapes for migratory prey.

Acknowledgements

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Glossary

Antipredator response: any response by a prey animal that reduces mortality risk (e.g., flee, travel in a group, change coloration).

Fitness rewards: outcomes of activities that increase an individual's lifetime reproductive success (e.g., the acquisition of energy from foraging).

Migration: animals engaging in persistent directional movement to a new location that repeats cyclically. Applies over any spatial or temporal scale and repetition can occur within or across generations (Dingle 2014; Cohen and Satterfield 2020). Inclusive of daily zooplankton migrations to one-way insect migrations to annual, roundtrip migrations of birds, fish, and ungulates.

Migration corridor: the area or habitats used as migrants travel between different locations (or destinations).

Migration destination: the areas or habitats on either end of the migration corridor. Often for breeding and wintering, spawning and growth, but could also include distinct habitats for diel migrations (e.g., different water depths).

Mortality risk: the realized probability of being killed by a predator. Mortality risk is driven by predator abundance and habitat features but also varies based on prey antipredator responses (Gaynor et al. 2019).

Perception: the ability of prey to detect and process information about risk from cues in the environment. The perception of mortality risk (sometimes called "danger") may differ from resulting mortality risk due to the effectiveness of antipredator responses (Gaynor et al. 2019).

Predation landscape: the pattern of spatial and temporal variation in predation across the migratory life cycle. Includes both the risk and response landscapes.

Predator cue: Information that indicates mortality risk. Cues can originate from a predator (e.g., visual, olfactory, auditory), other animals (e.g., alarm cues or calls), or the environment (e.g., risky or safe habitats).

Response landscape: the pattern of spatial and temporal variation in prey antipredator responses across the migratory life cycle. One component of a predation landscape.

Risk landscape: the pattern of spatial and temporal variation in mortality risk across the migratory life cycle. One component of a predation landscape.

Box 1. Restoring Predation Landscapes to Restore Ecosystem Processes

Management of top predators alters risk and response landscapes with consequences for communities and ecosystems. The interaction of wolves (*Canis lupus*), an apex predator, and migratory herds of elk (*Cervus canadensis*) in Yellowstone National Park, WY, USA exemplifies these interactions (Kauffman et al. 2007; Boyce 2018). Elk occupy high elevation plateaus with abundant forage in

summer and migrate to lower elevation ranges with less snowfall in winter. Wolves overlap elk distributions in winter but cannot follow elk in summer to higher elevations because they are constrained by denning sites. Wolves were extirpated from Yellowstone National Park by 1926 causing a decrease in mortality risk on the winter ranges for migratory herds of elk. Elk increased in abundance and behaviorally responded by using more areas of the park with ecological consequences of heavy herbivory that reduced abundance and distribution of preferred forage, especially woody plants such as cottonwood (*Populus balsamifera*), willow (*Salix* spp.), and aspen (*P. tremuloides*) (Figure IA).

In 1995, wolves were reintroduced to the park. At first, mortality risk increased spatially, following wolf territories, and elk behaviorally responded by avoiding wolf territories (Figure IB). As wolf populations rapidly increased, mortality risk increased and became widespread. Elk could no longer spatially avoid wolves completely. Instead, elk used habitat selection to avoid the riskiest habitats where wolves have greater hunting efficiency (i.e., riparian corridors, aspen stands) and to seek prey refuges (i.e., open areas, dense coniferous forests) (Figure IC). Therefore, restored wolf predation increased the magnitude and distribution of risk for migratory elk on the winter range. The spatial distribution of risk affected the distribution of elk responses, which in turn influenced ecosystems. Elk herbivory was more heterogeneous after wolf recovery – some areas in the park experience heavy elk herbivory while other areas, now avoided by elk, have experienced a release from herbivory, regeneration of vegetation, and expansion of willow, cottonwood and

aspen. This vegetation response in turn has allowed recovery of a diversity of species associated with wetland vegetation such as songbirds, waterbirds, beavers (*Castor canadensis*) and their predators. Wolf extirpation and recovery in Yellowstone National Park highlights changes in the risk landscape over time and space, which affected the distribution and strategies of elk responses with resulting ecological consequences.

Box 2. Predation of Migratory Prey Shapes the Movement of Nutrients Among Ecosystems

Migratory species move matter and nutrients between ecosystems, and predators shape these net movements by altering the number, size (or mass), and elemental composition of their prey (Luhring et al. 2017). The net movement of materials among ecosystems can be modeled as a function of migratory species biomass determined by population numbers (N) and individual mass (Figure I). If the relative number of individuals entering and exiting one location (N_{Out}/N_{In}) balances with the relative body size of those individuals ($Mass_{In}/Mass_{Out}$), there is no net movement of biomass into or out of the focal ecosystem. This is denoted by a Zero Net Transfer Isocline (Figure I). In most situations these values will not perfectly balance, and the result is a net movement of matter across ecosystem boundaries.

For anadromous salmon (*Oncorhynchus* spp.), many small juveniles move matter out of freshwater ecosystems, and fewer large adults return from the ocean to reproduce and die in freshwater. The large body size of adults relative to juveniles,

often results in a net influx of matter and nutrients from the ocean into freshwater (Figure IA). Marine predators, such as killer whales (*Orcinus orca*), can influence the flux of nutrients because they reduce the numbers (N_{In}) and body size ($Mass_{In}$) from size-selective predation of adult salmon, potentially shifting the system from one of "net import" into freshwater to one of "net export" (Figure IA) (Ohlberger et al. 2019).

For pond-breeding amphibians, many large metamorphosing juveniles leave ponds for the terrestrial environment, and even more, but smaller eggs are later deposited back in ponds by breeding adults (unlike salmon, breeding adult amphibians do not generally die after reproducing and therefore do not leave their entire body mass in the breeding ground) (Regester et al. 2006). The relatively large body size of juveniles compared to eggs usually makes this system one of "net export" of matter from the pond to the terrestrial environment (Figure IB). Stoichiometry also differs between life stages and juveniles export more calcium than returns with eggs. Ponds vary in the density of aquatic predators, which reduce the number of juveniles leaving the pond (N_{Out}). Predation in the aquatic habitat, therefore, shifts the system closer to one of "net import" into freshwater (Figure IB). Overall, predation on migrants alters the transfer of matter and nutrients across ecosystem boundaries, potentially affecting migrant populations and communities that receive migratory subsidies.

Box 3. Manipulating Predation Landscapes to Control Invasive Species

Risk and response landscapes provide alternative routes for conservation efforts. For native migratory species, efforts are aimed at restoring the balance between landscapes. However, landscapes can also be intentionally manipulated and disrupted to manage pestilent migrants. The parasitic sea lamprey (*Petromyzon marinus*) is invasive to the Laurentian Great Lakes where it imperils several ecologically, economically, and culturally important native fishes. In spring, adult lamprey cease parasitic feeding and migrate into rivers to spawn. Managers apply pesticides to these rivers to kill larval lamprey, thereby, acting as a super-predator and manipulating the risk landscape for sea lamprey. Pesticides cause substantial population declines, but incur some unintended environmental impacts (Lennox et al. 2020).

An alternative strategy is emerging that manipulates the response landscape. To reduce pesticide applications, managers could trap and remove lamprey; however, baited traps are not effective because lamprey do not feed while migrating. During upstream migration, adult sea lamprey are preyed upon by mammals, such as raccoons (*Procyon lotor*) and otters (*Lontra canadensis*) (Figure IA). Injured sea lamprey tissue releases an alarm cue that disperses downstream and guides conspecifics away from the risky shoreline (Figure IB). Scientists are developing an alternative management strategy that uses conspecific alarm cues to direct adult lamprey into traps for removal (Figure IC). Cues are released in the river on the opposite side from a trap to “push” sea lamprey away from where they perceive

predation risk towards the trap, resulting in 70% of migrants entering the trap (Hume et al. 2020). Because sea lamprey use social information to inform their antipredator behavior, manipulating alarm cues alters the response landscape to achieve management goals, providing an environmentally safe alternative to pesticides.

Figures

Figure 3.1 Predators Consuming Migratory Prey (A) Sandpipers (*Calidris mauri*) mitigate predation risk from peregrine falcons (*Falco peregrinus*) by avoiding high risk areas or increasing the speed of migration (Hope et al. 2014, 2020); (B) adult salmon (*Oncorhynchus* spp.) are heavily consumed by bears (*Ursus* spp.) in narrow, shallow streams that serve as pinch points (Quinn et al. 2017); (C) elk (*Cervus canadensis*) migration reduces predation on summer ranges, despite increasing predation in the migration corridor (Hebblewhite and Merrill 2007); (D) Mormon crickets (*Anabrus simplex*) use safety in numbers during migration as an antipredator response to minimize consumption by birds and rodents, but which also increases their risk of being preyed upon by parasitic wasps (Sphecidae) (Srygley and Lorch 2016). Photo credits: Joachim Bertrands (A), Tom Quinn (B), Daniel R. Stahler/NPS Photo (C), Robert Srygley/USDA-ARS (D)

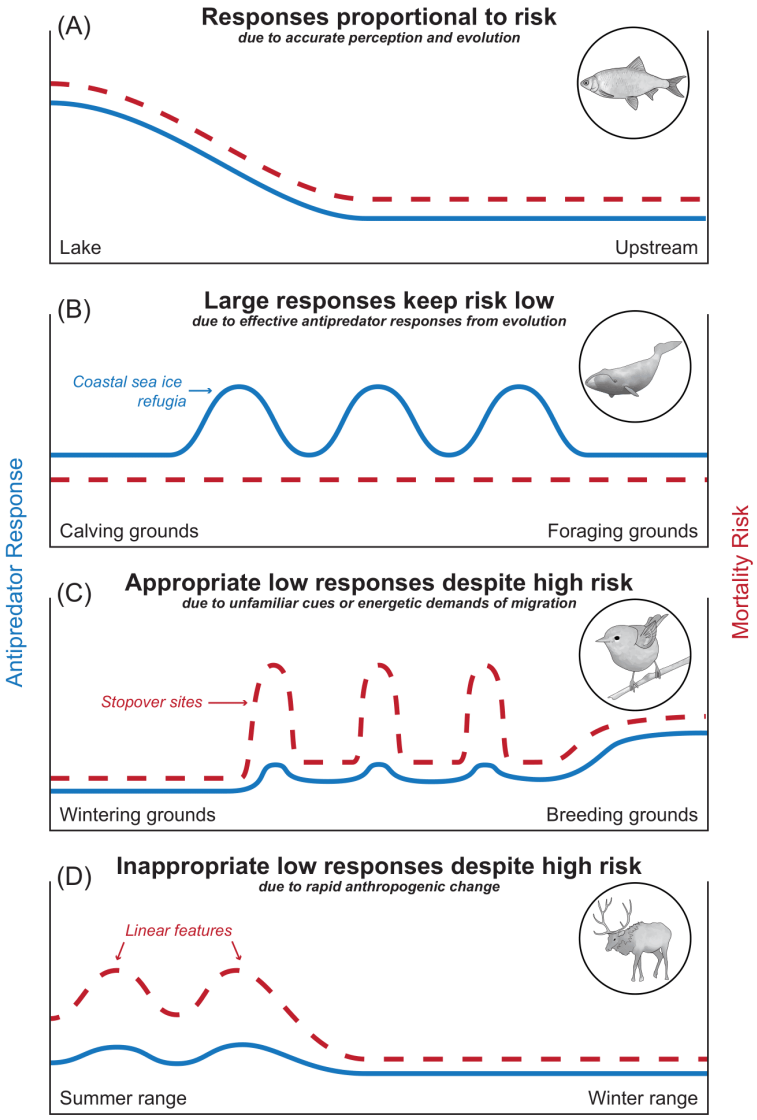

Figure 3.2 Predation Landscapes of Risk and Response. Landscapes of risk (dashed red line) and response (solid blue line) across the range of a migration route in space and time. Each panel represents a different relationship between mortality risk, antipredator response, and migratory challenge as illustrated by an empirical example. (A) Freshwater roach (*Rutilus rutilus*) feed in productive lake environments, which also have many predators (high-risk, high-reward), and evolved antipredator responses, which include increasing the propensity to migrate and departing early to the safety of streams (Hulthén et al. 2015). (B) Bowhead whales (*Balaena mysticetus*) effectively keep

mortality risk from killer whales (*Orcinus orca*) low by associating with coastal refugia when killer whales are nearby (Matthews et al. 2020). (C) Long-distance migratory birds use stopover sites to refuel energy stores, prioritizing energy intake over reducing their mortality risk (McCabe and Olsen 2015). (D) Migratory caribou (*Rangifer tarandus*) are especially vulnerable to predation by carnivores along man-made linear features in snow-free habitats to which they have minimal antipredator responses (DeMars and Boutin 2018; Dickie et al. 2020).

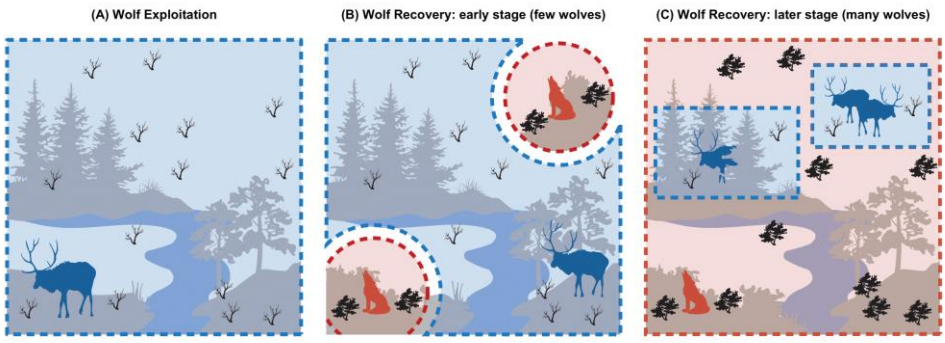

Figure 3.3 Risk and response patterns over time and space for migratory elk. Blue areas represent elk distribution and red areas represent wolf ranges. Black foliage denotes regeneration of vegetation. (A) When wolves were extirpated, elk had wide distributions and exhibited high herbivory across the park. (B) When wolves were first reintroduced, elk spatially avoided wolf territories and vegetation regenerated where elk were absent. (C) As wolf populations recovered, risk became widespread and elk shifted their strategy to avoid risky habitats (riparian and aspens) and preferentially occupied safer habitats (conifers and open grasslands).

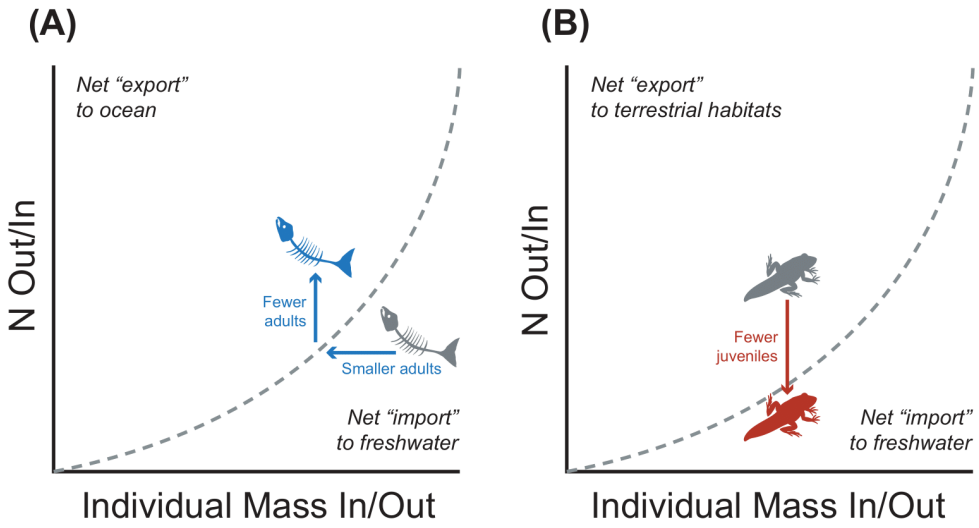

Figure 3.4 Conceptual plot of net ecosystem transfer in migratory species modified by predation. The dashed line indicates the Zero Net Transfer Isocline where exports equal imports of migratory prey biomass. Gray symbols (salmon carcass and metamorphosing frog) represent the hypothetical starting net ecosystem flux, arrows represent changes driven by predation, and colored symbols denote the new net ecosystem flux. (A) Anadromous salmon shift to the left from size-selective predation and up from predation on adults, changing from a system of net "import" to "export". (B) Pond-breeding amphibians shift down from predation on juveniles leaving the pond, changing from a system of net "export" to "import".

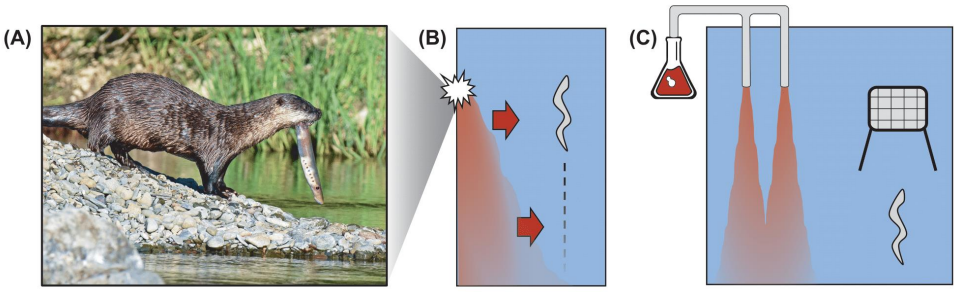

Figure 3.5 Lamprey responses to natural and manipulated alarm cues. A North American river otter kills a sea lamprey on the shoreline (A) causing alarm cues to be emitted from the damaged tissue that guides migrants around the risky area (B). Collecting alarm cues from lamprey tissue and pumping it into a stream allowed scientists to 'push' 70% of migrants to the entrance of the trap (C). Photo credit: Talia Rose.

Conclusion

Migratory animals are concentrated, conspicuous, and predictable in space and time making them especially vulnerable to predation (Furey et al. 2018). Through both consumption and changes to prey behavior, predators affect migratory prey from behavior to populations to communities (Sabal et al. 2021). ***Tradeoffs between risk and reward*** and ***ecological constraints*** are ubiquitous across all organisms and shape patterns and outcomes of predator effects. This dissertation explored how unique tradeoffs and constraints of migratory prey, involving energetic-demands and optimal timing of migration and traversing heterogeneous and unfamiliar habitats, influence predator effects to migratory prey behavior, ecology, and evolution.

In Chapter 1, I developed a new extension of economic escape theory applicable for directionally moving animals across species. The model generates qualitative, testable predictions for how migrants perceive risk balanced by opportunity costs of lost rewards. I connected antipredator behavior in directionally moving animals to movement, allowing a quantitative measurement of perceived risk across a variety of antipredator behaviors, scales, and species. Furthermore, lost rewards for moving prey can include immediate energetic and opportunity costs, but also future opportunity costs due to changes in arrival timing. The importance of linking antipredator behavior to movement to migratory timing has broad applicability and important potential consequences to migration behavior and fitness.

Additionally in Chapter 1, I conducted a behavioral assay to empirically test predictions of my economic escape theory model. I found juvenile Chinook salmon reaction to predator cues was context dependent on prior predator experience with more experienced wild salmon reacting more strongly than hatchery salmon. This illustrates how absence of experience presents an ecological constraint to appropriate antipredator responses. Learning is important to react to predators and suggests a potential behavioral mechanism for low hatchery survival (Berejikian et al. 1999). Finally, this experiment showcases how my economic escape theory model can be used in practice to evaluate qualitative predictions about how animals respond to risk.

In Chapter 2, I conducted another behavioral assay to examine how juvenile Chinook salmon antipredator behavior was influenced by salmon origin, overhead shade, and habitat structure. Shade caused salmon to perceive heightened risk and shift their escape tactic compared to direct sun. Once again, tradeoffs between risk and reward resulted in context dependent antipredator decisions in a migratory prey. Interestingly, salmon origin and structure did not have a significant effect on antipredator behavior, although they are often more important factors in non-migratory settings (Diehl 1988; Ajemian et al. 2015). This predicated an idea that unfamiliar and heterogeneous habitats of the migration corridor may constrain migrant antipredator responses and result in patterns that differ from non-migratory life stages.

In Chapter 3, I wrote a review paper to extend the theory, examples, and consequences from Chapters 1 and 2 across taxa and ecological scale. I used generalizable frameworks of "risk – perception – response" and "predation landscapes" to synthesize concepts and patterns across migratory insects, zooplankton, amphibians, fish, birds, and mammals. I identified common migratory challenges affecting tradeoffs and constraining ecological outcomes. Migrants face highly heterogeneous risk in habitat type and predator communities. This results in varied and often unfamiliar predator cues, constraining accurate perception of risk and promoting a reliance on social information. Behavioral responses are often context-dependent either from constraints or to balance the high energetic demands of migration, and it is common for antipredator behavior in migrants to affect migration timing.

Further in Chapter 3, I examined how humans are disrupting predator-migratory prey interactions through myriad activities (e.g., introduced species, pollution, altered habitats). These disruptions are concerning as migrants provide ecosystem services including pest control for agricultural crops and pollination (birds, bats, insects), fishing, hunting, and wildlife viewing, and commercial and subsistence harvest (Semmens et al. 2011). Predators also promote healthy ecosystems with diverse public benefits (Dobson et al. 2006). The review culminates with creative conservation suggestions to restore healthy predation landscapes including habitat restoration using dynamic protected areas, manipulating sensory ecology to promote

prey antipredator behavior, and creating artificial refuges for vulnerable migratory life stages.

The empirical research in Chapters 1 and 2 also has important management implications specific to ecologically, economically, and culturally valuable salmon populations. Chapter 1 suggested that predator conditioning in hatcheries could promote learning and consequently more accurate antipredator responses in hatchery salmon. Chapter 2 examined how habitat features affected salmon antipredator behavior and suggested the potential importance of pairing shade with in-water structure to reduce perceived risk. Both Chapters 1 and 2 highlight the conservation risks of assuming studies with hatchery salmon are representative of wild salmon and studies with non-migratory life stages are representative of actively migrating life stages.

This dissertation advances our understanding of how predators shape migratory prey behavior, ecology, and evolution through the tradeoff between risk and reward and unique ecological constraints. I examined these themes using diverse methods from theory to field experiments to syntheses across taxa, starting with individual decisions scaling up to patterns in behavior, populations, communities, and evolution. This research advances our understanding of animal migrations and predator-prey interactions to advance the conservation of ecologically and economically important and amazing migratory animals.

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