RESEARCH ARTICLE

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

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Abstract

1. Prey evaluate risk and make decisions based on the balance between the costs of predation and those of engaging in antipredator behaviour. Economic escape theory has been valuable in understanding the 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 behaviour causes a change in travel speed (the distance to a destination divided by the total time to reach that destination). Cryptic or cautious antipredator behaviour 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 behaviour, 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 behavioural 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, whereas 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.

1 | INTRODUCTION

Prey adjust their behaviour to balance the trade-off between predation risk and the costs of engaging in antipredator behaviour (Lima & Dill, 1990). These predator-induced behavioural decisions are important because they can influence population dynamics and community structure (Matassa & Trussell, 2011; Preisser, Bolnick, & Benard, 2005; Werner & Anholttt, 1993). Economic escape theory provides a framework to understand this trade-off (Cooper & Blumstein, 2015; Ydenberg & Dill, 1986). Escape theory has been used to make predictions about various behavioural responses of prey (e.g. at what distance to flee, when to emerge from refuge) relevant across a range of animal taxa (Cooper & Frederick, 2007; Hugie, 2003; Martin, 1999). The magnitude of the behavioural 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 behavioural 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 behaviour (Samia, Blumstein, Stankowich, & Cooper, 2016; Stankowich, 2008; Stankowich & Blumstein, 2005). 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 behaviour remains an important gap in economic escape theory.

Moving animals are conspicuous and vulnerable to predators (Furey, Armstrong, Beauchamp, & Hinch, 2018; Hammerschlag, Morgan, & Serafy, 2010). 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 (Banks, Norrdahl, & Korpimaki, 2000; Clarke et al., 1993). Furthermore, predation pressure on moving animals is often exacerbated by human activities such as introduction of non-native 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 to reach their destination—for example, anadromous fish migrating through rivers must pass by relatively stationary predators to reach the ocean (Dalton, Ellis, & Post, 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; Poupart et al., 2019; Ripperger, Kalko, Rodríguez-Herrera, Mayer, & Tschapka, 2015). Relevant over many spatial and temporal scales, animals moving towards 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, Marschall, & Swanson, 2004), diel vertically moving fish (Busch & Mehner, 2011) and ungulate movements to and from water sources (Cain, Owen-Smith, & Macandza, 2012). Directionally moving prey include both individual animals travelling 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 threefold. 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 behavioural assay with migratory juvenile Chinook salmon *Oncorhynchus tshawytscha* that vary in their past predator experience.

2 | MATERIALS AND METHODS

2.1 | Adapting escape theory to model directionally moving prey behaviour

2.1.1 | 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 behaviour 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 van

Breukelen, Hootsmans, & van Wieren, 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, Lim, Kang, Armenta, & Blumstein, 2017). The general question escape theory models ask is as follows: 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 behaviour (Brown, 2003). When moving prey must eventually make it to their destination, engaging in antipredator behaviour 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 behaviours 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 behaviour 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, Grigg, Hamlin, & Garrott, 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; Cimprich, Woodrey, & Moore, 2005; Ciuti et al., 2012; Yoder et al., 2004). These cautious or cryptic antipredator behaviours will slow travel speed (or delay time to the destination) compared to if they did not need to use antipredator behaviour. Therefore, in our model, we can measure directionally moving prey's reaction to predation risk by how much their antipredator behaviour changes their travel speed (or time to destination).

Our model considers only changes in travel speed that are caused by antipredator behaviour. 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 travelling quite fast overall. Our model does not predict this 'baseline' travel speed, but rather the change in travel speed that is 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 behaviour with and without cues of predation risk.

2.1.2 | Cost curves

In economic escape theory, the trade-off between predation risk and opportunity costs (e.g. missed foraging, mating opportunities)

determines prey behaviour (Figure 1a). For directionally moving prey, we assume the cost of changing travel speed (i.e. cost of antipredator behaviour) is either energetic (e.g. to fight or flee) or due to mismatched arrival time at the destination. If antipredator behaviour 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 behaviour as opportunity costs. These opportunity costs increase with the magnitude of the antipredator behaviour because prey have larger energetic or timing costs (Figure 1b).

This model only uses changes to travel speed that are caused by antipredator behaviour. Therefore, the cost of not changing travel speed is the cost of no antipredator behaviour 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 (Figure 1b). Predation risk is assumed to decrease when prey engage in antipredator behaviour, which changes their travel speed (Figure 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 behaviour 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 behaviour (Figure 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 behaviours slow prey down compared to prey speeding up to reduce encounter time with predators (Figure 1c). For study questions focused only on the amount of risk perceived or in systems where antipredator behaviours are fixed, then modelling unidirectional predictions are appropriate (Figure 1b). However, prey may have multiple antipredator behaviours, 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 (Figure 1c). Opportunity costs could be high if prey arrive early or late at their destination, and various antipredator behaviours 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 behaviours in different directions. Cost curves, however, are likely not symmetrical. If either cost curve varies in slope between speeding up and slowing down (or between different escape strategies), then there will be two intersection points of varying height (Figure 1e). For example, if predators are more likely to detect prey if they speed up to flee compared to slow down to be

FIGURE 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 behaviours at intersection points

(a) FID model (Ydenberg & Dill, 1986)

(b) Directionally moving prey model − magnitude

(c) Directionally moving prey model − direction

(d) Sensitization hypothesis

(e) Directionally moving prey model − non-symmetrical
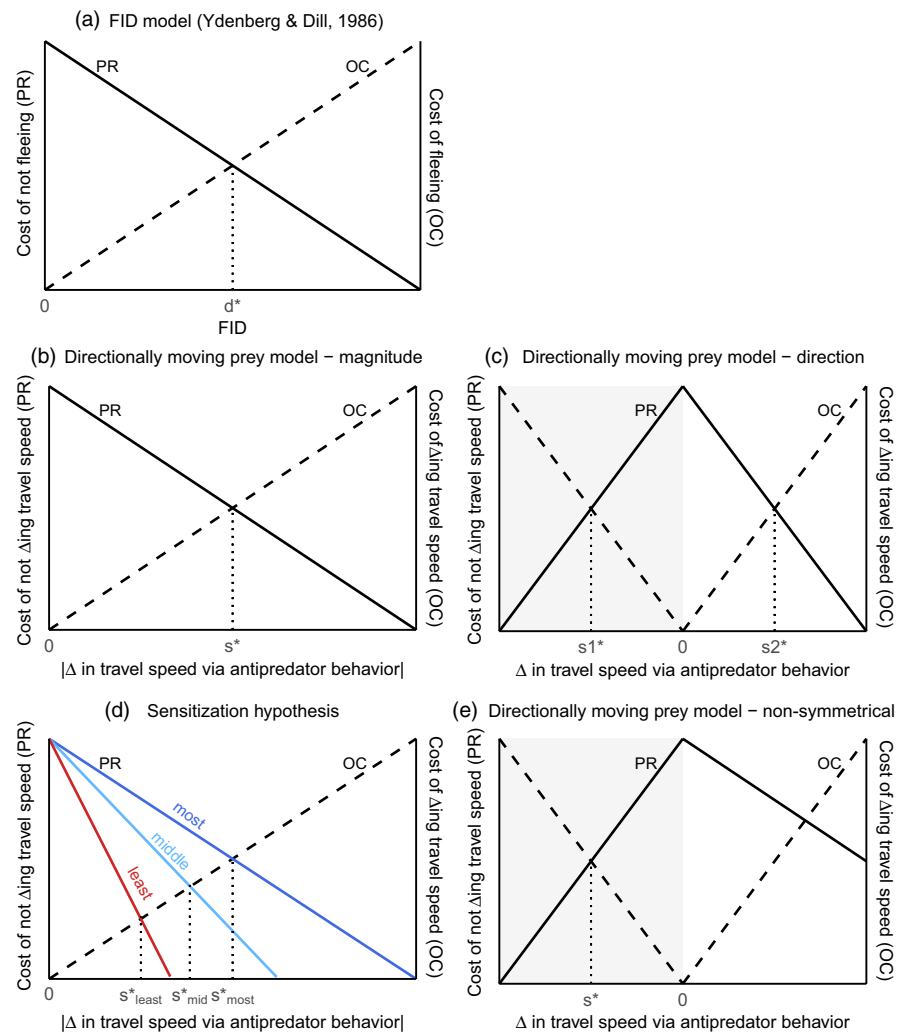
cryptic, then predation risk is higher in the positive direction (Ciuti et al., 2012; Figure 1e). Natural selection will favour prey that exhibit the behaviour at the lower intersection point, which minimizes fitness costs, and there will be only be one predicted optimal behaviour in a particular direction.

Thus, our escape theory model for directionally moving prey can make qualitative and ordinal predictions about two behavioural aspects: (a) the magnitude of change in travel speed infers the amount of perceived risk and (b) 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 behaviours.

2.1.3 | 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 Figure 1) or curvilinear, and the model is only useful in generating predictions when cost curves

intersect. We also assume that antipredator behaviour changes travel speed, and there are numerous empirical observations that support this link (Dodson, Tollrian, & Lampert, 1997; Hope, Lank, Smith, & Ydenberg, 2011; Luhring et al., 2016; Melnychuk & Welch, 2018; Proffitt et al., 2009). 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 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 behaviour (e.g. FID) and can be applied to various antipredator behaviours (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 behaviours 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, Eichhorn, van Langevelde, & Bauer, 2010). A potential consequence of summing behaviour 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 behaviour patterns.

2.1.4 | 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 behaviours. 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 behaviour. 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 (Figure 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 (Figure 1d).

2.2 | Experimental study

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 behaviour. Specifically, we asked (a) do juvenile salmon engage in antipredator behaviours that change their travel speed? and (b) 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 behaviour, and that more experienced prey would react more strongly to predation risk (Figure 1d).

2.2.1 | 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, Skalski, Brandes, & Fuller, 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 & 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 travelled downstream because moving prey passing stationary predators have increased predator encounter rates with distance travelled (Anderson et al., 2005). Furthermore, piscivore abundance often increases as rivers become larger and warmer downstream (Vannote, Mishall, Cummins, Sedell, & Cushing, 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 behaviour with the greatest magnitude under predation risk, followed by wild-upstream, and lastly hatchery salmon (Figure 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 & Deangelis, 2000) or slow down to evaluate risk (Kelley & Magurran, 2003; Vehanen, 2003).

This experiment spanned 15–26 May 2017, and behaviour 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 5 months when salmon are between 35- and 120-mm fork length (FL; Merz, Workman, Threloff, & Cavallo, 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 & 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 behavioural trials. Travelling from upstream to downstream capture locations, juvenile salmon on the Lower Mokelumne River encounter an increasing abundance of non-native predators (including largemouth bass) as measured by fish community surveys (Del Real, Rible, Shillam, & Saldate, 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, Hayes, Merz, & Setka, 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 protocol PALKE1701.

2.2.2 | Behavioural 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 behaviour. 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-µm 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 ± 0.06 m/s) 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 (Figure 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, 1.2 and 2.1 m from the starting end (hereafter referred to as antennas 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 behavioural 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 odour cues are commonly used indicators of predation risk in behaviour experiments (Ferrari, Gonzalo, Messier, & Chivers, 2007). The enclosure design precluded some juvenile salmon natural antipredator behaviours, such as schooling, hiding in substrate and movements perpendicular to flow, but did allow predator inspection, vigilance and cautious behaviour, which are common fish antipredator behaviours over small spatial and temporal scales (Kelley & Magurran, 2003).
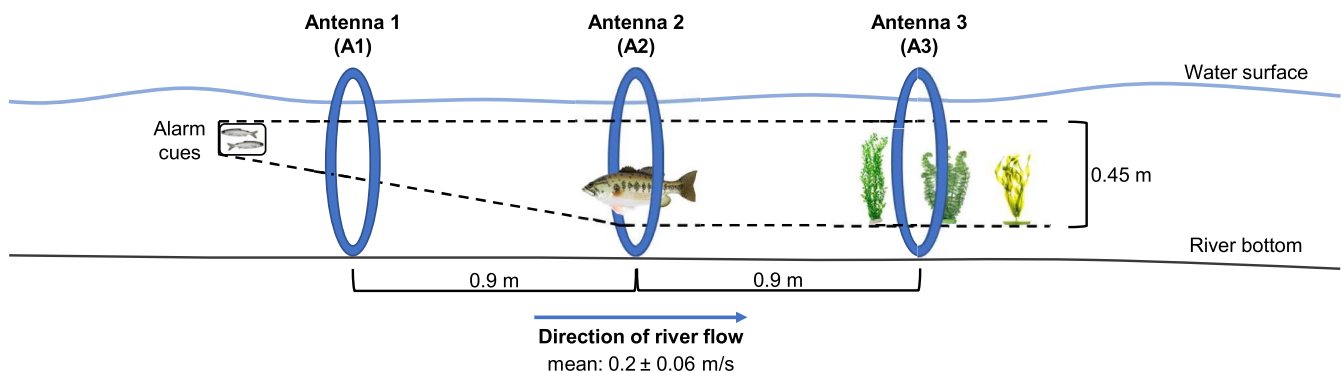

FIGURE 2 Diagram of experimental mesh enclosure including positions of antennas, model predator (at A2), conspecific alarm cues (before A1) and artificial habitat (at A3). Juvenile salmon were released between the alarm cues and antenna A1

Prior to behaviour 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 × 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 ($M \pm SD$: 1.5 ± 0.8%; Brown et al., 2010). All salmon were allowed at least 30 min to recover after tagging, but all recovered within a few minutes, and there were no tagging mortalities. To begin a behaviour 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 1 min. At that time, the container lid was removed, and the container was rotated 90°, 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 min 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.

2.2.3 | Data analysis

To evaluate our study questions, namely (a) do juvenile salmon change their travel speed under predation risk and (b) 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 (travelling 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 min. 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 behaviour. 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 & 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 09:00 and 15:00 hr 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).

3 | RESULTS

We ran 63 juvenile Chinook salmon through paired behaviour 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 ± 0.3°C), air temperature (mean: 27.8 ± 5.2°C), surface water velocity (mean: 0.2 ± 0.06 m/s) 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 travelling 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 antennas A2 to A3 was 129 ± 134 s or travelling at 0.04 ± 0.06 m/s. Travel time was highly right-skewed with most salmon travelling quickly through the enclosure (Figure S1). There were significant interactions between predator treatment and salmon group and between split and salmon group influencing salmon travel speed (Figure 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 (Figure 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 (Figure 3).

TABLE 1 ANOVA table for mixed-effects cox model on salmon time to event

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

*$p < 0.05$;

TABLE 2 Linear contrasts and effect sizes on salmon speed (time to event) upon significant interactions between salmon groups with predator treatment and split

	COXME: speed		Effect size	
Salmon group	Z-ratio	p	Hedge's g	Magnitude[a]
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

[a]Thresholds defined by Cohen (1992).
*$p < 0.05$; [†]$p < 0.1$.

4 | 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 behaviour 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 behaviour 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 trade-offs that influence how directionally moving prey respond to predation risk and to make qualitative predictions about behavioural patterns across ecosystems and taxa.

Wild juvenile salmon changed travel speed in response to predation risk, supporting the prediction that antipredator behaviour affects travel speed in directionally moving prey. Many antipredator behaviours 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 behaviours in fish (Kelley & 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,

FIGURE 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 antennas A1 and A2, while the right plot shows travel speed changes from A2 to A3. Vertical lines represent standard errors
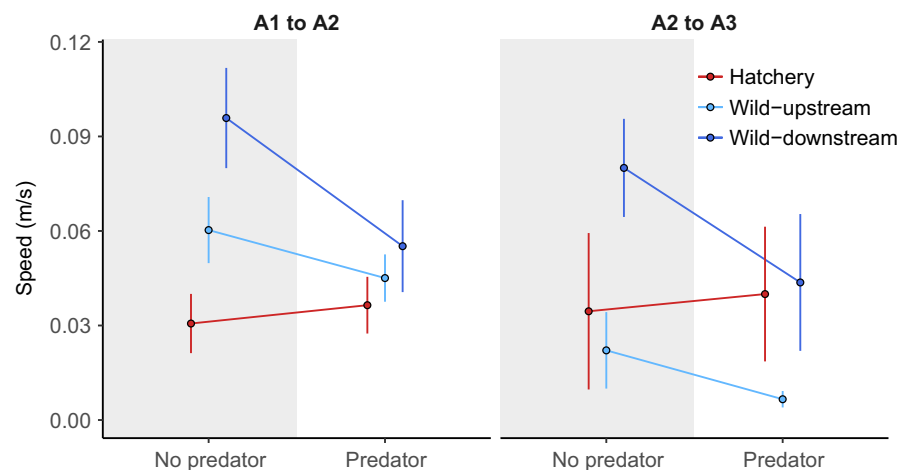
presumably to reduce encounter time with predators (Dodson et al., 1997; Luhring et al., 2016). At larger scales, forest birds translocated away from their home territories, travelled more slowly returning home as forest cover decreased, perhaps because birds took longer routes to avoid large gap crossings with high predation risk (Bélisle, Desrochers, & Fortin, 2010). Juvenile sockeye salmon *Oncorhynchu 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 behaviours 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 behaviours, 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 (Hawkins, Magurran, & Armstrong, 2008; Kihslinger & Nevitt, 2006; Sundström, Petersson, Höjesjö, Johnsson, & Järvi, 2004). 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, Grimes, Royer, & Donohoe, 2007), it is important to understand how rearing environment and exposure to predator cues change antipredator behaviour. 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 & Richardson, 2010; Parsons et al., 2018; Shannon, Crooks, Wittemyer, & Fristrup, 2016).

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 behavioural 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 to 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 & McCarthy, 2002; Sutton & 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 refuelling and subsequently travel speed in migratory birds (Hope, Lank, & Ydenberg, 2014).

Behavioural 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 behaviours, 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 behaviours. Also, prey behaviour 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 behaviours that speed up and slow down travel speed. In this situation and others, there will always be challenges in simplifying complex antipredator behaviours to a single, measurable escape response. Despite these challenges, examining prey behaviour 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 behaviours; therefore, the framework exists to tease apart behavioural 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 behaviours adapted to chronic predation risk. Animals can migrate in groups to dilute

risk (Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016; Furey et al., 2016; Reynolds, Sword, Simpson, & Reynolds, 2009) and follow specific routes to avoid predators (Ydenberg, Butler, & Lank, 2007). These are generally evolved strategies that are not initiated by proximate predator cues. Prey commonly use behaviours 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 travelling 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 & Blumstein, 2015). Behavioural responses under predation risk are important because they can subsequently affect populations and communities (Matassa & Trussell, 2011; Preisser et al., 2005). 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 behaviours 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 behaviour advances economic escape theory and improves our general understanding of how animals assess predation risk.

AUTHORS' CONTRIBUTIONS

M.C.S., E.P.P. and J.E.M. designed the study; M.C.S. ran the experiment and performed analyses; M.C.S. and S.H.A. developed the conceptual model; M.C.S. wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.