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Risk-sensitive information gathering by cyprinids following release of chemical alarm cues

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In aquatic environments, chemical cues released during a predator attack reliably inform prey about the presence of predation risk. Prey with information about predation risk are more successful in surviving encounters with predators than are unwary prey. To remain prepared for attack, prey should continue to monitor the status of predation risk, presenting a behavioural trade-off for prey: increased distance from areas labelled with alarm cues reduces exposure to predation risk but also reduces access to information about predation risk. In two laboratory experiments we used the presence and absence of water flow in a laboratory fluvarium to test alarm response and subsequent risk-sensitive information gathering by zebrafish (*Danio rerio*). In response to chemical alarm cues, fish significantly reduced activity and increased use of shelters. In the absence of flow, fish sought out the shelter nearest the cue source. In the presence of flow, fish preferred to seek shelter downstream, but not upstream, of the cue source. This allowed fish to gather information about predation risk from a relatively safe distance. In a field experiment on natural populations of stream fishes, fish avoided areas where chemical alarm cues were released (versus blank water control) but primarily because they avoided the region immediately upstream of the cue source. Fish use of the area immediately downstream of cue release did not decrease. Taken together, these laboratory and field data are consistent with a trade-off between risk avoidance and information gathering.

Much of behavioural decision making is guided by public information released as a natural consequence of ecological interactions. Public information is valuable to receivers in several important contexts ranging from habitat selection to cultural evolution (Danchin et al. 2004). In aquatic environments, public information about predation risk takes the form of various chemical cues released during successive stages of the predation sequence (sensu Lima & Dill 1990; Smith 1992; Wisenden & Chivers 2006).

Animals place a high priority on gathering information about predation risk. Predator inspection behaviour, where prey approach a predator directly, has stimulated a large literature (e.g. Dugatkin & Godin 1992). However, little work has been done on the inspection of indirect indicators of predation risk, such as sources of chemical cues. Information is valuable only to the degree to which it is accurate, and, because of the temporally dynamic nature of predation risk, accuracy requires frequent updating. Gathering information about predation risk presents a trade-off in that the most accurate information is obtained where risk is greatest. Here, we test for a trade-off between information gathering and risk avoidance using zebrafish (*Danio rerio*) in 1.8 m long fluvaria in which water flow could be turned on or off. Chemical alarm cues derived from conspecific skin extract either diffused slowly from the point of release (no flow) or was carried the length of the fluvarium by water current (flow). When water flow was turned off, chemical alarm cues were detectable only at the shelter nearest the site of cue release. If the function of an alarm reaction is only to minimize predation risk, then zebrafish in both flow treatments should seek refuge in distant shelters. If alarm reactions include overt risk avoidance traded off against the benefits of information gathering, then fish in the no-flow treatment should tolerate risk to access information by seeking refuge in the shelter nearest the location of cue release.

Laboratory experiments afford control and power to detect biological effects, but their contrived nature may result in unnatural or spurious behavioural responses (Irving & Magurran 1997). Therefore, we repeated our laboratory experiments on field populations of minnows occupying natural river systems. Together, these data combine the experimental power of the laboratory setting with the ecological realism of the field setting.

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METHODS

Laboratory Fluvaria

The zebrafish, *Danio rerio*, is a lotic cyprinid native to India and a model organism for molecular genetics (Engeszer et al. 2007). Zebrafish have a well-documented antipredator response to chemical alarm cues from conspecifics (e.g. Waldman 1982; Suboski et al. 1990; Hall & Suboski 1995; Korpi & Wisenden 2001). Study animals were acquired from commercial suppliers and housed in 190-litre holding tanks at the aquatic research facility at Minnesota State University Moorhead (MSUM).

Individual fish were placed into one of two identical fluvaria. The fluvaria were rectangular troughs, 30 cm wide and 2.44 m in length with a viewing pane along one side (Fig. 1). Water depth was maintained at 7.5 cm. A stack of drinking straws (diameter = 6.0 mm) immediately downstream of the point of water entry stabilized turbulence. A second identical stack of straws at the downstream end immediately before the drain left a 180 cm section of open stream between two visually identical ends. In the second iteration of this experiment the downstream stack of straws was not used, creating 210 cm of usable stream. Lines drawn on the front viewing pane divided the tank into 18 (experiment 1) or 21 (experiment 2) 10 cm sections. The fluvarium bottom was covered with a thin layer of silica sand that provided a smooth bottom to minimize retention of chemical cues as they passed through the stream system (Ferner et al. 2009).

A short length (ca. 20 cm) of rigid plastic tubing for injecting test stimuli descended vertically from a special holder designed for this purpose midway across the width of the fluvarium, ending mid-column between the water surface and substrate. A 2 m length of flexible plastic airline hosing attached to the rigid tubing extended to the floor in front of the tank where experimenters could surreptitiously inject test stimuli without disturbing the test subject. Before pre-stimulus observations began, a 60 ml syringe was used to withdraw and discard two draws of 60 ml of tank water through the stimulus injection tube to rinse it. A third draw of 60 ml of tank water was taken and retained to flush the control test stimulus (10 ml of dechlorinated water). A fourth draw of 60 ml of tank water was retained in another syringe to flush the alarm cue stimulus (10 ml of skin extract). Rigid and flexible tubing used for stimulus injection were replaced for every trial.

Experimental Protocol

The experimental protocol was identical for both iterations of the laboratory experiment. A single zebrafish was placed into a fluvarium and allowed at least 24 h to acclimate. Flow was on and recirculating through the reservoir during this time. Each fish was observed over three consecutive observation periods. Pre-stimulus data were collected for 3 min. Activity, horizontal position and shelter occupancy were recorded. Activity was tallied as the sum of the number of times the fish passed one of the lines drawn on the front viewing pane (spaced 10 cm apart). Horizontal position was recorded as a scan sample of the 10 cm areas occupied by the fish at 15 s intervals. At the time of the scan sample, we also recorded whether the fish occupied a shelter. When the pre-stimulus period was complete, we redirected the outlet of the stream tank from the reservoir to the floor drain. Thus, introduced chemical stimuli now passed only once through the fluvarium before being flushed permanently from the system. We then immediately began injecting 10 ml of dechlorinated tap water (control) through the stimulus injection tube, followed by the flush of previously retained 60 ml of tank water. Stimulus injection required about 1 min to complete. Activity, horizontal position and shelter use were then recorded for 3 min. This observation period was called the post-water period. When that observation was complete, we injected 10 ml of skin extract solution containing alarm cues followed by 60 ml of previously retained tank water to flush alarm cues into the tank. Stimulus injection required about 1.5 min to complete. We recorded activity, horizontal position and shelter use again for 3 min (post-alarm period).

Description of Flow Parameters and Fate of Odour Plumes

In the absence of flow, injected stimuli diffused a mean ± SE distance of 34.9 ± 0.98 cm ($N = 10$ dye tests) from the point of release (i.e. to include the nearest shelter, but not the distant one (s)) within the 3 min observation period. Food colouring dye released within the 0–10 cm section reached the first shelter

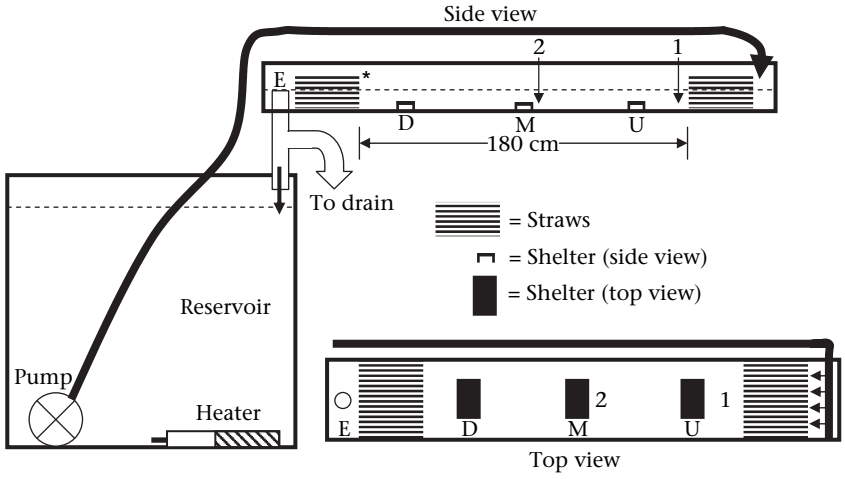

Figure 1. Design of the artificial stream systems used in the present study showing a 580-litre reservoir from which water was pumped to one end of a rectangular trough with one side made of glass. The 180 cm open stream section in the centre was divided into 18 zones, 10 cm each, by a grid (not shown) drawn on the front viewing pane. A stack of drinking straws at the upstream end served as a collimater to stabilize turbulence and create uniform current velocity. *A second stack of straws at the downstream end was used in experiment 1 only. The drain returned water to the reservoir during acclimation periods. During data collection water was directed to the floor drain so that test stimuli were not recirculated. In experiment 1, shelters occupied the zone between the 30 and 40 cm sections, and 150–160 cm downstream of the straws. In experiment 2, shelters were placed at 30, 100 and 170 cm. Side view and top view are shown. E = end pipe; D = downstream shelter; M = middle shelter; U = upstream shelter.