Article

Sender and receiver experience alters the response of fish to disturbance cues

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Abstract

Predation is a pervasive selection pressure, shaping morphological, physiological, and behavioral phenotypes of prey species. Recent studies have begun to examine how the effects of individual experience with predation risk shapes the use of publicly available risk assessment cues. Here, we investigated the effects of prior predation risk experience on disturbance cue production and use by Trinidadian guppies Poecilia reticulata under laboratory conditions. In our first experiment, we demonstrate that the response of guppies from a high predation population (Lopinot River) was dependent upon the source of disturbance cue senders (high vs. low predation populations). However, guppies collected from a low predation site (Upper Aripo River) exhibited similar responses to disturbance cues, regardless of the sender population. In our second experiment, we used laboratory strain guppies exposed to high versus low background risk conditions. Our results show an analogous response patterns as shown for our first experiment. Guppies exposed to high background risk conditions exhibited stronger responses to the disturbance cues collected from senders exposed to high (vs. low) risk conditions and guppies exposed to low risk conditions were not influenced by sender experience. Combined, our results suggest that experience with background predation risk significantly impacts both the production of and response to disturbance cues in guppies.

Key words: disturbance cues, ecology of information, perceived risk, predator–prey interactions, Trinidadian guppy

The ability to reliably assess local predation threats allows prey to balance the often conflicting demands of reducing predation risks while still maintaining sufficient time and energy to engage in other fitness related activities such as foraging (Lima and Dill 1990; Ferrari et al. 2010). Chemosensory cues provide valuable sources of public information regarding the identity and intensity of local predation threats (Kats and Dill 1998), allowing for context appropriate behavioral trade-offs. For example, wood mice Apodemus sylvaticus reduce foraging behavior when in the presence of predatory chemical cues (Sunyer et al. 2013). Likewise, desert isopods Hemilepistus reaumuri use the presence vs. absence of the odor of scorpion Scorpio palmatus to make fine-scale risk assessments (Zaguri et al. 2018).

Within aquatic systems, prey are widely known to assess predation risk directly from chemosensory information originating from the predator (Kats and Dill 1998) or through cues released by conspecific and/or heterospecific prey-guild members (Vavrek et al. 2008; Ferrari et al. 2010). Perhaps most studied among aquatic prey are the damage-released chemical alarm cues, which are released via mechanical damage, as would occur during a predator attack (Chivers and Smith 1998; Brown 2003; Ferrari et al. 2010). Given the mechanism of release, these cues are reliable indicators of local predation risks (Chivers et al. 2007; 2012) and can elicit strong species-typical antipredator responses in nearby conspecifics and heterospecific prey-guild members (Ferrari et al. 2010, Chivers et al. 2012).
In addition to the damage-released alarm cues, many aquatic prey species rely on disturbance cues as sources of local threat assessment (Ferrari et al. 2010). Disturbance cues differ from the alarm cues, as they are non-injury released sources of risk assessment information, released in urine or across the gill epithelium of aquatic vertebrates when stressed or disturbed (Wisenden et al. 1995; Vavrek and Brown 2009; Brown et al. 2012; Abreu et al. 2016). Thus, disturbance cues would be released (and potentially detected) much earlier in the predation sequence (Wisenden et al. 1995) and elicit short-term increases in predator avoidance behavior (i.e., increased shoaling and decreased area use in guppies, Goldman et al. 2019). Given that they are released prior to an attack by a predator, disturbance cues are argued to function as early warning cues (Wisenden et al. 1995; Ferrari et al. 2010). Disturbance cues are widely distributed across phyla, as they have been identified in a diverse range of species, such as invertebrates (Hazlett 1985, 1990a, 1990b; Nishizaki and Ackerman 2005; Siepielski et al. 2016), amphibians (Kiesecker et al. 1999; Gonzalez et al. 2010; Crane and Mathis 2011) and fish (Wisenden et al. 1995; Manassa et al. 2013; Bett et al. 2016; Fulton et al. 2017; Goldman et al. 2019).

A growing body of research demonstrates that past experience with predation shapes how prey respond to damage-released alarm cues (Brown 2003; Ferrari et al. 2009; Brown et al. 2013). For example, guppies from high predation risk populations exhibit stronger antipredator and more threat-sensitive (Brown 2009, 2014) responses to standardized predation threats compared to conspecifics from low predation risk populations. Indeed, recent studies demonstrate that exposure to conditions of elevated predation risk for even a few days is sufficient to induce “high risk behavioural phenotypes among prey” (Brown et al. 2013, 2015; Crane and Ferrari 2016; Mitchell et al. 2016). Given that alarm cues are “honest and reliable” indicators of acute predation risks (Brown 2003; Chivers et al. 2012), it is perhaps not surprising that prey may alter their response to these cues based on recent experience. However, Chivers et al. (2007) demonstrated that alarm cue senders do not show similar plasticity in the production and release of alarm cues; fathead minnows reared under high versus low predation conditions did not differ in the production of alarm cues.

Recent experience with predation risk has also been shown to influence how prey respond to disturbance cues. Wood-frog tadpoles Lithobates sylvaticus adjust behavioral responses according to background risk experience, exhibiting all-or-nothing responses among high-risk receivers, regardless of sender risk level (Bairos-Novak et al. 2017). However, tadpole receivers with low-risk experience exhibited stronger responses to the disturbance cues of high versus low-risk senders. In addition, Bairos-Novak et al. (2019a) have shown that the release of disturbance cue can be influenced by familiarity among group members in the fathead minnow. Thus, it appears that while the effects of ambient predation risk is limited to plasticity of the response in the case of damage-released alarm cues (Chivers et al. 2007; Brown et al. 2009), prey may adjust both the release of, and response to disturbance cues (Bairos-Novak et al. 2019a, 2019b).

Here, we test the effects of background predation risk on both the production of and response to disturbance cues in Trinidadian guppies in wild-caught guppies from populations with different background predation risk conditions (Experiment 1) and in a common laboratory population, in which we manipulated background risk experimentally (Experiment 2). Initially, we predict that guppies from a high predation risk population should respond to disturbance cues more intensely and produce disturbance cues that elicit a stronger response compared to conspecifics from a low predation risk population. Second, if predicted responses of wild caught guppies are due to predation experience (and not population-specific differences), we predict the same response patterns in a laboratory strain of guppies experimentally exposed to high versus low background risk conditions.

Materials and Methods

Experiment 1: Effects of sender and receiver source population

Under laboratory conditions, we tested the effects of ambient predation risk on both the production and response to conspecific disturbance cues in wild-caught Trinidadian guppies. We collected female guppies from the Lopinot and Upper Aripo Rivers, Trinidad, using a 3-mm mesh seine net. The Lopinot River is a high predation stream, with a diverse predator guild including pike cichlids (Crenicichla sp.), blue acara Andinoacara pulcher, brown coscarub Cichlasoma taenia, and wolf fish Hoplias malabaricus (Deacon et al. 2018). The Upper Aripo is characterized as low predation site with no aquatic predators of adult guppy present (Deacon et al. 2018). Guppies were transported to the University of the West Indies, St Augustine, Trinidad, and housed in 100-L glass aquaria. These holding tanks were kept at ~26°C, under a 12:12 h light: dark cycle and guppies were fed twice daily with commercial flake food and freeze-dried tubifex.

In order to generate disturbance cues (and the odor of undisturbed guppies), shools of 10 Lopinot River or Upper Aripo River guppies were placed into 20L tanks and allowed to acclimate for 24h. Tanks were aerated, continuously filtered and wrapped in white plastic to prevent visual disturbance. We passed a realistic predator model (Feyten et al. 2019) connected to a glass rod through the tank for 60 s, being careful not to contact the fish. The 14 cm long model (3D printed in polycarbonate) was hand painted to emulate a pike cichlid, a common guppy predator. After passing the model through the tank, we waited 60 s and gently mixed the water and collected ~100 mL to be used as a disturbance cue. We collected all cues immediately before use in laboratory trials. As a control, we collected water samples (odour of undisturbed conspecifics) from the sender tanks prior to presenting the model predator. This protocol has been shown to be a reliable way to collect disturbance cues (Vavrek et al. 2008; Goldman et al. 2019; Bairos-Novak et al. 2019a). We generated cues from a total of five ‘sender’ shools from each population (i.e. each sender group was used to test 2 replicates for cue × focal receiver population combination). Mean ± SD size of cue senders was 21.60 ± 2.23 mm SL for Lopinot River guppies and 21.02 ± 2.53 mm SL for Upper Aripo guppies.

Behavioral observations were conducted in a series of 20 L glass aquaria, filled with 18L of dechlorinated tap water (~24°C, 12:12 L: D cycle). We affixed a single airstone to the back wall of the tank and attached an additional 1.5 m length of airline tubing to facilitate stimulus injection. We placed shools of three female guppies into testing tanks and allowed ~2 h to acclimate prior to testing (as in Brown and Godin 1999; Brown et al. 2009). We tested guppies in shools, as singleton guppies typically exhibit high levels of baseline stress (i.e., pacing and darting behavior, personal observations). Mean ± SD size at testing was 23.50 ± 1.89 mm SL for Lopinot River guppies and 22.15 ± 1.79 mm SL for Upper Aripo guppies. Observations consisted of a 5 min pre-stimulus and a 5 min post-stimulus observation period. Immediately following the pre-stimulus observation period, we injected 10 mL of disturbance cue...
Table 1. Summary of treatments and number of shoals tested per treatment combination

| Receivers | Senders | Stimulus | N   |
|-----------|---------|----------|-----|
| Lopinot River | Lopinot River | Disturbance cue | 10 |
| Upper Aripo | Lopinot River | Disturbance cue | 10 |
| Upper Aripo | Lopinot River | Undisturbed conspecific cue | 10 |
| Upper Aripo | Lopinot River | Undisturbed conspecific cue | 10 |
| Upper Aripo | Upper Aripo | Disturbance cue | 10 |
| Upper Aripo | Upper Aripo | Undisturbed conspecific cue | 10 |
| Upper Aripo | Upper Aripo | Undisturbed conspecific cue | 10 |

Each test shoal consisted of 3 female guppies. See text for details for number of stimulus sender shoals.

We used a total of 95 non-gravid (visually assessed) female guppies as alarm cue senders (mean ± SD standard length = 26.2 ± 0.57 mm and body depth = 4.7 ± 0.14 mm). Senders were euthanized via cervical dislocation (in accordance with Concordia University Animal Research Ethics Protocol #30000255). We immediately removed the head, tail (at the caudal peduncle), and internal visceral tissues. The remaining tissue was placed into 100 mL of chilled distilled water and then homogenized and filtered through polyester filter floss. We added distilled water to achieve our desired final volume. We collected a total of 181.6 cm² of skin (diluted to a final volume of 1210 mL). Alarm cues were frozen in 40 mL aliquots at ~20°C until required. Damage-released chemical alarm cues at this concentration are known to elicit reliable increases in predator avoidance behavior (increased shoal cohesion and reduced vertical area use) in guppies (Brown et al. 2009; 2013).

To create high versus low levels of background risk among receivers, we placed groups of size matched female guppies (16 shoals of 3 guppies each; N = 48 per group) into 40 L flow-through bins. Each bin contained a gravel substrate and a single air stone affixed to the back right and was held at ~21°C. Focal fish ‘bins’ were exposed to 10 mL of conspecific alarm cue (high risk) or 10 mL of distilled water (low risk) twice per day for 5 days (as in Brown et al. 2013; 2015). Approximately 30 min after exposure to a pre-conditioning cue, we conducted a partial water change (~50% volume). We fed each group of fish twice daily throughout the conditioning phase. We replicated this process three times, with each “block” of high- versus low-risk focal guppies yielding four shoals of three guppies for each treatment combination (disturbance cue vs. odour of undisturbed conspecifics from high-risk and low-risk senders).

Using a similar procedure, we manipulated background risk for cue senders. Two shoals of 20 size-matched female guppies (one high-risk shoal and one low-risk shoal, replicated four times for each risk level) in 37 L aquaria containing a gravel substrate and an air stone. We increased the number of senders per tank (20 vs. 10) due to the larger tank volumes used in order to keep the relative concentration of disturbance cues similar. As above, sender tanks were exposed to either 10 mL of alarm cue or distilled water, twice daily for 5 days. We conducted ~50% water changes 30 min following the introduction of a cue. As we replicated sender groups four times, each sender group yielded disturbance and undisturbed cues for three test replicates per treatment combination. Disturbance cues and the odor of undisturbed conspecifics were collected as described above.

Behavioral observations were conducted as described above, with the exception that shoals of guppies were tested in 37 L glass aquaria (filled with 20 L of dechlorinated tap water, ~24°C, 12:12 L: D cycle). Mean (± SD) size at testing 23.9 ± 7.4 mm. We calculated the proportional change in shoaling index and area use scores for each replicate (as per Mitchell et al. 2016). As focal guppies were pre-exposed to risk conditions as groups, we cannot consider them as truly independent. To account for this non-independence, pre-exposure round was included as a nested factor using ANOVAs (SPSS V24.0). Due to some guppies escaping test tanks during the acclimation period, final sample sizes ranged from 9 to 12 per treatment combination (Table 1). As above, observations were made blind to treatment and the order of testing was randomized throughout the experiment.
**Results**

**Experiment 1**

Our overall analysis revealed a significant main effect of focal population and stimulus, as well as a significant three-way interaction among the effects of sender and focal populations and stimulus type for the proportional change in shoaling index (Table 2; Figure 1A). Regardless of treatment combination, guppies appeared to increase shoal cohesion in response to disturbance cues (Figure 1A). However, both Lopinot (high risk) and Upper Aripo (low risk) River guppies exhibited stronger responses to the disturbance cues collected from Lopinot River senders, with the greatest response in the Lopinot receivers–Lopinot sender treatment combination (Figure 1A). For the proportional change in area use, we found only a significant effect of stimulus (disturbance cue vs. the odour of undisturbed conspecifics, Table 2; Figure 1B). We observed similar reductions in area use regardless of disturbance cue sender or focal population (Table 2; Figure 1B).

**Experiment 2**

Our overall analysis suggests that the behavior of guppies pre-exposed to high versus low levels of background risk follows a similar pattern found among wild caught guppies from high versus low predation risk populations (Experiment 1). We found no significant effect of pre-conditioning block (nesting factor, \( P > 0.05 \) for both shoaling index and area use; Figure 2, Table 3). We found a significant three-way interaction for the proportional change in shoaling index (Figure 2A, Table 3). As with wild caught guppies, laboratory guppies exhibited an increase in shoal cohesion in response to disturbance cues, regardless of background risk treatment. However, guppies pre-exposed to the high-risk background treatment exhibited greater increases in shoaling index in response to disturbance cues from high risk vs. low risk senders (Figure 2A; Table 3). Similar to the response of wild-caught guppies, we found a significant decrease in proportional area use in response to disturbance cues (Figure 2B; Table 3). However, the significant receiver risk level x stimulus interaction term (Figure 2B; Table 3) suggests that high risk guppy receivers exhibited stronger responses to disturbance cues than did low risk receivers. As above, sender experience had no effect on the observed change in area use (Figure 2B; Table 3).

**Discussion**

Our first experiment shows the combined effects of sender and receiver experience on the response to disturbance cues. Guppies from the Lopinot (high-risk) showed stronger overall responses compared to guppies from the Upper Aripo (low-risk). However, the response of Upper Aripo guppies did not differ based on the experience of the sender, whereas the response of Lopinot guppies differed based on sender experience. Our results suggest that under high-risk conditions, there is an interacting effect of receivers and senders, but under low-risk conditions there is no effect of senders. The results of

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Table 2. Results of ANOVAs on the proportional change in shoaling index and area use for guppies tested in experiment 1

|                | \( F \)  | \( Df \) | \( P \)   |
|----------------|---------|---------|----------|
| Shoaling index |         |         |          |
| Sender         | 0.34    | 1, 72   | 0.56     |
| Focal          | 4.09    | 1, 72   | 0.047    |
| Stimulus       | 48.33   | 1, 72   | <0.001   |
| Sender x Stimulus | 1.87   | 1, 72   | 0.18     |
| Focal x Stimulus | 8.04   | 1, 72   | 0.006    |
| Sender x Focal | 0.04    | 1, 72   | 0.84     |
| Sender x Focal x Stimulus | 5.78 | 1, 72   | 0.019    |
| Area use       |         |         |          |
| Sender         | 1.05    | 1, 72   | 0.31     |
| Focal          | 0.33    | 1, 72   | 0.57     |
| Stimulus       | 37.21   | 1, 72   | <0.001   |
| Sender x Stimulus | 0.11   | 1, 72   | 0.92     |
| Focal x Stimulus | 0.94   | 1, 72   | 0.34     |
| Sender x Focal | 0.19    | 1, 72   | 0.67     |
| Sender x Focal x Stimulus | 0.27 | 1, 72   | 0.61     |

Sender population (high vs. low predation risk), focal population (high vs. low predation risk) and stimulus (disturbance cue vs. odor of undisturbed conspecifics) were included as independent variables. \( N = 10 \) per treatment combination.

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Figure 1. Proportional change in shoaling index (A) and proportional change in area use (B) for guppies collected from high predation (Lopinot) and low predation (Upper Aripo) streams and exposed to the disturbance cue (solid circles) or odor of undisturbed guppies (open circles) from Lopinot or Upper Aripo senders. \( N = 10 \) per treatment combination. Horizontal bars denote means.
our second experiment compliment those of Experiment 1, demonstrating that when background risk is induced, we also observed a combined effect of sender and receiver experience. It is interesting to note that the observed effects of sender and receiver experience were only seen in one of two behavioral measures (shoaling index). Given that disturbance cues are released earlier in the predation sequence, they may be perceived as a lower risk form of information compared to sources of risk assessment such as alarm cues (Wisenden et al. 1995; Ferrari et al. 2010). Recent studies have shown that the response to disturbance cues is concentration dependent (Vavrek and Brown 2009; Goldman et al. 2019), consistent with previously documented threat-sensitive responses to damage-released alarm cues (Dupuch et al. 2004; Brown et al. 2006, 2009). It is possible that the low risk senders in the current experiment were simply producing lower quantities (concentration) of disturbance cues and that our observed response patterns are simply due to “detectable concentrations” of disturbance cues. However, Brown et al. (2009) demonstrate that while guppies from high-risk populations show stronger maximal responses to high concentrations of conspecific alarm cues, guppies from low-risk populations show significant response (increased shoaling and reduced area use) to much lower concentrations.

Our results represent the first demonstration that prey fish can modify the intensity of their antipredator responses proportionately to chemosensory cues based on information provided by the prior experience of both cue senders and receivers. We cannot rule out population-specific differences in Experiment 1. It is possible that population differences in, for example, competition or foraging opportunities may shape the response patterns observed. However, the results of experiment 2, in which we induce risk in a single population, show analogous response patterns and provide support for our initial hypothesis. Alongside our results, recent studies show that background risk affects receivers of chemosensory cues (Brown et al. 2009; Bairos-Novak et al. 2017). Our results extend this, showing that experience also shapes how senders produce information. Previous studies show that background risk does not alter alarm cue production (Chivers et al. 2007). However, as disturbance cues are released earlier in the predation sequence than alarm cues (Wisenden et al. 1995), senders may have greater plasticity in disturbance cue production. Bairos-Novak et al. (2017) demonstrated interacting effects between background risk and response to disturbance cues in woodfrog tadpoles, although the observed responses were all-or-nothing. Our results suggest that there is a graded response based on interacting experience. However, guppies increase the intensity of their antipredator responses based on sender experience only when the receivers were high-risk. Therefore, the effects of a sender’s experience only matter for high-risk receivers. This suggests that high-risk receivers may be more sensitive to information that is conveyed by the sender.

Consistent with previous findings (reviewed in Ferrari et al. 2010), our current results suggest high risk receivers may benefit from enhanced predator avoidance responses to disturbance cues.

![Figure 2. Proportional change in shoaling index (A) and proportional change in area use (B) for guppies pre-conditioned to high versus low predation risk and exposed to the disturbance cue (solid circles) or odor of undisturbed conspecifics (open circles) from high versus low risk senders. Receiver risk treatment denoted as HR-R (high risk receivers) versus LR-R (low risk receivers). N = 9–12 per treatment combination. Horizontal bars denote means.](image-url)
Perhaps more interesting, our results suggest that the release of disturbance cues by senders is also shaped by background predation risks. Recently, Bairos-Novak et al. (2017) have argued that disturbance cues may function as a source of social information among prey regarding local predation risks and that senders benefit by releasing disturbance cues. Consistent with this, we found that increases in shoaling behavior were greatest among high risk guppies in response to disturbance cues from high risk senders. If disturbance cues are, at least in part, released voluntarily by senders (Bairos-Novak et al. 2019a; Crane et al. manuscript in review), our current results suggest that prey exposed to high risk conditions may benefit from releasing more (or more potent) disturbance cues. Senders should benefit from enhanced antipredator responses among nearby prey guild members.

There is growing interest in understanding the ecology of information in predator–prey interactions (Schmidt et al. 2010; Luttrell and Trussell 2013; Magrath et al. 2015; Evans et al. 2016). Aquatic environments tend to be extremely heterogeneous, which makes it important to quantify the degree to which variation within the environment shapes information. Moreover, given the high degree of fission-fusion nature of guppy shoals (Croft et al. 2003; Wilson et al. 2014), it is reasonable to expect considerable variation in recent predation experience among shoalmates. Our results demonstrate that predation risk alters the information conveyed by disturbance cues, and that prey benefit from responding to these cues and may also benefit from their release. Therefore, we highlight the importance of disturbance cues in predator–prey interactions and specifically, how they can play a crucial role in the predation sequence. Combined with recent studies (Bairos-Novak et al. 2017; 2019a, 2019b; Goldman et al. 2019), we provide evidence for the use of disturbance cues as a model to investigate the ecology of information in predator–prey interactions. Future studies should investigate whether these cues are in fact a signaling system to warn prey guild members, whether they can also be utilized as an antipredator tactic by senders to increase survival and the degree to which other ecological factors shape their information content (i.e., competition or diet).

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