Local predation risk shapes spatial and foraging neophobia patterns in Trinidadian guppies

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Received on 10 September 2015; accepted on 8 December 2015

Abstract

The “dangerous niche” hypothesis posits that neophobia functions to reduce the cost of habitat use among animals exposed to unknown risks. For example, more dangerous foraging or higher competition may lead to increased spatial neophobia. Likewise, elevated ambient predation threats have been shown to induce phenotypically plastic neophobic predator avoidance. In both cases, neophobia is argued to reduce the cost of living associated with ecological uncertainty. Here, we test the hypothesis that ambient predation shapes both neophobic predator avoidance and spatial and foraging neophobia in Trinidadian guppies. Guppies were exposed to a novel foraging arena paired with a known cue (conspecific alarm cue), a novel cue (lemon odor), or a stream water control in three streams differing in ambient predation risk. We demonstrate that guppies from a high-predation-risk stream exhibited risk-averse foraging patterns regardless of the chemical stimulus presented (high spatial neophobia) and that those from a low-predation-risk stream were only risk-averse when the foraging arenas were paired with conspecific alarm cue (lower spatial neophobia). Those tested in the intermediate-predation-risk stream were consistently intermediate to the high-risk vs. low-risk populations. Our study suggests that ambient predation risk shapes both neophobic predator avoidance and space-use patterns and that neophobia may function as a “generalized” response to ecological uncertainty.

Key words: phenotypic plasticity, predator recognition, foraging, predator recognition, predator-prey interactions, Trinidadian guppies.
Trinidadian guppies _Poecilia reticulata_ from high-predation, but not low-predation, sites exhibit increased predator avoidance (i.e., increased shoaling, reduced movement) when exposed to novel chemosensory cues. Similar neophobic predator avoidance response patterns can be induced by relatively short periods of exposure to high-risk conditions. For example, juvenile convict cichlids _Amatitlania nigrofasciata_, wood frog _Lithobates sylvaticus_ tadpoles, and Trinidadian guppies exposed to high-risk conditions for as little as 3 days exhibit increased neophobic responses to novel chemical cues (Brown et al. 2013, 2015). Moreover, the strength (Brown et al. 2014a) and retention (Brown et al. 2015) of induced neophobic responses are proportional to the intensity of the background level of risk. These induced neophobic responses to novel risky cues should allow prey to reduce their vulnerability to predation while still allowing sufficient behavioral plasticity to respond to local variation in risk levels.

To date, neophobic predator avoidance and spatial neophobia have typically been examined separately. The dangerous niche hypothesis, however, predicts that neophobia would serve as a generalized response to any factor that increases ecological uncertainty. Thus, we would expect ambient predation risk to be linked to both neophobic predator avoidance and spatial neophilia. Prey populations exposed to unpredictable predation threats should respond to any novel cue as a potential threat (i.e., neophobic predator avoidance) and exhibit higher levels of spatial and foraging neophobia. Such a general neophobic response pattern should allow prey to reduce the costs associated with exploiting novel habitats. However, it remains unknown whether spatial and foraging neophobia is correlated with neophobic predator avoidance.

Here, we used direct observations under natural conditions to test the hypothesis that prey exposed to higher (vs. lower) levels of ambient predation risk will exhibit increased spatial and foraging neophobia. We exposed wild, free-swimming shoals of Trinidadian guppies to a novel foraging patch paired with one of three chemosensory cues: a known risky cue (damage-released alarm cue), a novel cue (lemon odor), or a stream water control in three streams varying in ambient predation risk. Previous studies have shown that guppies from populations exposed to high levels of risk demonstrated strong neophobic responses to novel odors, whereas those from low-risk populations were indifferent (Brown et al. 2013; 2014b). Guppies from populations of intermediate risk were also intermediate in their responses to novel odors (Brown et al. 2013). We predict that guppies tested in a high-predation-risk stream should show higher levels of spatial neophobia, regardless of the chemical cue presented. Conversely, we predict that guppies tested in a low-predation-risk stream should show increased spatial neophobia only in the presence of a known risky cue (conspecific alarm cues).

**Materials and Methods**

**Trial arenas**

We constructed foraging arenas consisting of a flat base and three upright sides using white corrugated plastic. Arenas measured $25 \times 25 \times 40\text{ cm} (L \times W \times H)$, with the base extending 15 cm beyond the open side. We inserted a 2 m length of standard airline tubing to allow for the injection of chemosensory stimuli (see below) approximately 5 cm from the bottom of the back wall of the arena. We positioned foraging arenas within 1 m of the shoreline at an approximate depth of 20 cm with the open end facing downstream. Arenas were held in position with stones along the back wall. Immediately before each trial, we placed a novel food item in the center of the arena. To generate the food blocks, we dissolved 85 g of unflavored gelatin in $\sim 450\text{ mL}$ of water and added 300 mL of flake food (NutraFin). The mixture was refrigerated and allowed to set at $\sim 4^\circ\text{C}$ overnight and transported to the field on ice.

**Chemical cues**

We tested the effects of three chemosensory cues: damage-released chemical alarm cues (known risk), lemon odor (novel “risk”), or stream water as a control. Damage-released chemical alarm cues are widespread among aquatic vertebrate and invertebrate prey species (Chivers and Smith 1998; Ferrari et al. 2010). Conspecific chemical alarm cues are honest and reliable indicators of risk (Chivers et al. 2012; Brown et al. 2014b) and elicit increased antipredator responses in guppies (Brown et al. 2009, 2014b). We generated alarm cues from 32 non-gravid female guppies (mean ± SD standard length $= 21.88 \pm 2.18\text{ mm}$). Cue donors were euthanized via cervical dislocation (in accordance with Concordia University Animal Research Ethics protocol). Due to their small body size, we used whole body extracts rather than skin extracts (Brown et al. 2009). After removing the head and tail, we immediately placed the remaining tissue into 100 mL of chilled dechlorinated water. We then homogenized the tissue samples, filtered through polyester floss, and diluted with dechlorinated water to the desired final volume and concentration ($0.1\text{ cm}^2\text{ mL}^{-1}$). We collected a total of $43.68\text{ cm}^2$ of tissue in a final volume of 430 mL. For the novel chemical cue (lemon odor), we diluted Badia™ (Doral, Florida, USA) lemon extract in dechlorinated water (6-mL lemon extract in 300-mL water; as in Brown et al. 2013). Conspecific alarm cue and lemon odor were frozen in 20-mL aliquots at $-20^\circ\text{C}$ and transported to the field on ice. Stream water controls were sampled _in situ_.

**Study sites**

Observations of focal shoals were conducted in discrete pools within three Trinidadian streams varying in ambient predation pressure. The Lower Aripo River is characterized as a high predation site (Croft et al. 2006; Botham et al. 2008), containing several species that actively prey on juvenile and adult guppies. Common predators include pike cichlid (_Crenicichla sp._), blue acara _Aequidens pulcher_, brown coscarub _Cichlasoma taenia_, wolf fish _Hoplias malabaricus_, and two-spot sardine _Astyanax bimaculatus_. The Upper Aripo River is characterized as a low predation site (Croft et al. 2006; Botham et al. 2008) as it contains Hart’s rivulus _Rivulus hartii_, and a freshwater prawn _Macrobrachium crenulatum_, which opportunistically prey on small, juvenile guppies (Endler and Houde 1995; Elvidge et al. 2010). The Tacarigua River is characterized as an intermediate-predation-risk stream, with a predator guild similar to that of the Lower Aripo River but at a lower density (Croft et al. 2006; Botham et al. 2008). Observations were conducted from the shoreline of slow-flowing pools within each of the three study streams. Observation sites were at least 10 m apart, and we moved upstream between observations to reduce the likelihood of repeated exposures to cues. Within any single pool, we only conducted one observation per chemical stimulus. Pool was included as a random factor in our statistical model (see below) to account for repeated observations (as in Elvidge and Brown 2012; Brown et al. 2013).

**Experimental protocol**

Trial sites were visually scanned before positioning the arena to ensure that at least five adult guppies were present within a 50 cm
radius of the trial arena. After a 1-min acclimation period after introducing the trial arenas, we began a 5-min observation during which we slowly injected 10 mL of one of the chemical cues followed by 60 mL of stream water through the airline tubing (as in Brown et al. 2013).

During the 5-min observation, we recorded the latency until the first guppy entered the arena, the latency to forage on the novel food patch (recorded from the onset of the trial) and the frequency of foraging attempts within the arena. In addition, we counted the number of guppies within a 50 cm downstream radius of the opening to the arena every 15 s. To account for differences in the number of guppies present, we converted foraging rates to per capita rates (foraging rate divided by mean number of guppies present). We performed $n = 12$ replicates for the alarm cue treatment in each of the three streams and $n = 19$ (Lower Aripo) and $n = 20$ (Upper Aripo and Tacarigua) for the novel cue and the control.

### Statistical analysis

To ensure normality, the latency to enter the novel foraging patch and the latency to forage were square-root transformed. After transformations, all data met the assumptions for parametric tests. We tested the effects of stream and stimulus (and the interaction) using univariate GLMs (SPSS v 22.0) for each of the dependent variables (latency to enter, latency to forage, number of guppies present, and per capita foraging rate). We included pool as a random factor in the overall analyses. Due to the presence of significant two-way interactions (see below), we further tested the effects of stimulus on all behavioral measures for each stream independently using univariate GLMs. We used Tukey’s Honest Significant Differences (HSD) to make post hoc comparisons between treatments within streams.

### Ethics standards

All work reported herein was conducted in accordance with Concordia University Animal Research Ethics protocol 30000255 and complies with all provincial and federal legislation. Research permits were approved by the Ministry of Food Production, Aquaculture Unit, Republic of Trinidad and Tobago.

### Results

Our overall analyses (Table 1) revealed significant stream × stimulus interactions in the latency to enter the arenas ($P = 0.018$), latency to forage ($P = 0.001$), and per capita foraging rates ($P = 0.014$). Pool had no significant effect as a random factor ($P > 0.05$ for all). For the mean number of guppies present, we found significant main effects of stream ($P < 0.001$) and stimulus ($P = 0.012$), but no significant interaction ($P = 0.63$). As above, pool had no significant effect ($P = 0.29$). To further investigate these main effects, we analyzed the effect of stimulus on the response of guppies within each stream independently.

In the high-predation stream (Lower Aripo), we found no significant effect of stimulus on any of the behavioral measures (Table 2; Figure 1). In each case, the response of guppies exposed to the high-risk cue (conspecific alarm cue) was similar to the response of those exposed to either the novel cue (lemon odor) or the stream water control. We found a decided different response pattern in the low-predation stream (Upper Aripo); both latency to enter and latency to forage were significantly higher when guppies were exposed to the conspecific alarm cue stimulus, with no difference between the novel cue and the water control (Table 2, Figure 1A,B). As in the Lower Aripo, there was no difference in the number of guppies present between treatments (Table 2; Figure 1C).

The responses of guppies tested in the Tacarigua River suggest a pattern intermediate to that found in the high- and low-risk streams. As in the Upper Aripo, Tacarigua guppies exposed to alarm cues took significantly longer to enter the novel foraging patch compared with those exposed to the novel odor or the water control (Table 2; Figure 1A). The latency to forage was longest for guppies exposed to alarm cues and shortest for those exposed to the water control. The latency to forage for guppies exposed to the novel odor was intermediate (Table 2; Figure 1B). Similarly, the per capita foraging rate was lowest for those exposed to the alarm cue stimulus and highest for those exposed to the water control, with an intermediate foraging rate among those exposed to the novel odor (Table 2; Figure 1C).

### Table 1. $P$-values and test statistics for the responses of Trinidian guppies to novel foraging arenas and chemical cues in three streams varying in predation level

|                          | $F$  | $df$ | $P$  |
|--------------------------|------|------|------|
| Latency to enter         |      |      |      |
| Stream                   | 8.90 | 2, 129 | < 0.001 |
| Stimulus                 | 12.91 | 2, 129 | < 0.001 |
| Stream × stimulus        | 3.10 | 4, 129 | 0.014 |
| Pool                     | 0.60 | 16, 129 | 0.79 |
| Latency to forage        |      |      |      |
| Stream                   | 8.22 | 2, 129 | < 0.001 |
| Stimulus                 | 13.68 | 2, 129 | < 0.001 |
| Stream × stimulus        | 5.02 | 4, 129 | 0.001 |
| Pool                     | 0.99 | 16, 129 | 0.48 |
| Guppies present          |      |      |      |
| Stream                   | 8.40 | 2, 129 | < 0.001 |
| Stimulus                 | 4.58 | 2, 129 | 0.012 |
| Stream × stimulus        | 0.65 | 4, 129 | 0.63 |
| Pool                     | 1.19 | 16, 129 | 0.29 |
| Per capita foraging rate |      |      |      |
| Stream                   | 2.17 | 2, 129 | 0.12 |
| Stimulus                 | 3.48 | 2, 129 | 0.034 |
| Stream × stimulus        | 3.27 | 4, 129 | 0.014 |
| Pool                     | 0.92 | 16, 129 | 0.55 |

### Table 2. $P$-values and test statistics from univariate GLMs on the effect of chemical stimulus on Trinidian guppies within each study stream

| Population              | $F$  | $df$ | $P$  |
|-------------------------|------|------|------|
| Lower Aripo (high predation) |      |      |      |
| Latency to enter        | 1.16 | 2, 47 | 0.32 |
| Latency to forage       | 1.64 | 2, 47 | 0.21 |
| Per capita foraging rate| 0.04 | 2, 47 | 0.94 |
| Guppies present         | 1.38 | 2, 47 | 0.26 |
| Tacarigua (intermediate predation) |      |      |      |
| Latency to enter        | 6.12 | 2, 49 | 0.004 |
| Latency to forage       | 7.94 | 2, 49 | 0.001 |
| Per capita foraging rate| 2.99 | 2, 49 | 0.06 |
| Guppies present         | 1.47 | 2, 49 | 0.24 |
| Upper Aripo (low predation) |      |      |      |
| Latency to enter        | 14.40 | 2, 49 | < 0.001 |
| Latency to forage       | 10.83 | 2, 49 | < 0.001 |
| Per capita foraging rate| 4.62 | 2, 49 | 0.014 |
| Guppies present         | 1.11 | 2, 49 | 0.34 |
Figure 1D). As with the other streams, there was no observed effect of stimulus on the number of guppies present (Table 2; Figure 1C).

**Discussion**

Consistent with the “dangerous niche” hypothesis (Greenberg and Mettke-Hofmann 2001; Mettke-Hofmann et al. 2013), our results suggest that as predation risk increases, prey exhibit higher levels of spatial and foraging neophobia, in addition to the previously documented neophobic predator avoidance (Brown et al. 2013, 2014a,b). Guppies in the high-predation-risk stream (Lower Aripo River) took longer to enter the trial arenas and to begin foraging, and did so at lower rates regardless of the chemosensory information available. Conversely, guppies in the low-predation-risk stream (Upper Aripo River) exhibited risk-averse spatial and foraging patterns only when the trial arena was paired with a known risky cue (i.e., conspecific alarm cues). When we paired the novel foraging arena with a novel chemosensory cue in the low-predation-risk stream, the latency to enter and forage decreased and the per capita foraging rate was highest when guppies were exposed to the novel cue, suggesting neophilic instead of neophobic response patterns. Finally, guppies in the intermediate-predation-risk stream (Tacarigua River) exhibited a mixed response. These results are consistent with those observed by Brown et al. (2013) for the predator.
avoidance patterns in the same three populations, with guppies under higher predation risk exhibiting neophobic responses to novel chemosensory cues.

Unpredictability in ecological risks arises when prey animals lack relevant or reliable information regarding the risks associated with a particular habitat (Dall et al. 2005; Ferrari et al. 2010; Mathot et al. 2012). When faced with such unpredictability, the overall “cost of living” to an individual should increase as the relative costs as associated with making an inappropriate behavioral decision would be greater. Although predation risk is often ascribed as a cost among neophobic populations, our study is one of the few to directly test the effects of ambient predation risk on neophobic space-use and foraging patterns. Three-spined sticklebacks (Gasterosteus aculeatus) from high-predation-risk ponds exhibited stronger spatial neophobia (measured by latency to approach a novel object) than conspecifics from lower risk ponds when tested under laboratory conditions but no effect of predation level in riverine populations (Brydges et al. 2008).

In agreement with other studies (Brown et al. 2013; 2014b; Mettke-Hofmann 2014), our current results suggest that neophobia may serve as a generalized response, reducing costs associated with unknown risks. Such a generalized neophobic response could provide prey organisms with the ability to reduce their overall costs of living under uncertain or changing conditions. Previous models suggest that increased foraging and/or competitive costs may influence the level neophobia in birds (Greenberg and Mettke-Hofmann 2001; Mettke-Hofmann 2014). We might also predict that increased competitive costs or increased unpredictability in the spatial or temporal availability of foraging opportunities would likewise result in increased neophobic predator avoidance. For example, prey forced to compete for limiting resources may incur increased costs from deferring early predator detection in favor of obtaining sufficient energy intake (Brown et al. 2005). Increased neophobic predator avoidance may reduce the costs of failing to respond to a potential predator among prey under highly competitive conditions.

Neophobia is potentially costly in that increased time spent avoiding risky situations may result in less opportunity to engage in other “fitness related” activities such as foraging, mating, and territorial defense (Lima and Dill 1990). As such, Brown et al. (2013) argued that neophobic predator avoidance should be a phenotypically plastic (i.e., inducible) response to variability in predation pressure. The current results extend this, suggesting that foraging and exploration patterns are similarly linked to ambient predation risk. The observation that guppies took longer to enter a novel foraging patch and longer to initiate foraging behavior under high-risk vs. low-risk conditions is consistent with increased vigilance under risky conditions. Such an increase in vigilance when confronted with a novel foraging opportunity could result in a short-term loss of energy acquisition. However, under risky conditions, this short-term loss would likely be offset by increased survival. Thus, it appears that phenotypically plastic neophobia may best be seen as a generalized response to uncertainty in ambient risk instead of a predator avoidance mechanism as suggested by Brown et al. (2013).

It is important to note that our study streams may differ in a number of ecological parameters besides predation risk levels. However, it is well established that predation risk in Trinidadian streams are linked to population-specific differences in behavior, morphology, and life history of guppies (Kelly et al. 1999; Kelly and Godin 2001; Reznick et al. 2001; Kelley and Magurran 2003; Croft et al. 2004; Magurran 2005). Although it is possible that the observed patterns may be due to differential foraging opportunities or competition levels (Reznick et al. 2001), the within-stream patterns are consistent with our neophobia hypothesis. For example, under high ambient predation risk conditions (lower Aripo), guppies treat known (high risk) and unknown (novel) chemical cues as similarly risky. However, under low-risk conditions (Upper Aripo), only the known cues are treated as risky. Further studies should attempt to account for between-stream differences in productivity and/or competitive interactions.

**Funding**

Financial support was provided by the Natural Sciences and Engineering Research Council of Canada and Concordia University to G.E.B. and Fond de recherch du Québec-Nature et technologies to C.K.E.

**Conflicts of interest**

The authors have declared no conflicts of interest.

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