

Article

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

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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.

Ecological uncertainty, broadly defined as the absence of complete information regarding local conditions (Dall et al. 2005; McNamara and Dall 2010), limits the ability of prey to adjust to novel habitats (Dall et al. 2005). Variability in the spatial and temporal availability of suitable foraging opportunities, intra- and interspecific competition and/or predation threats would be expected to increase ecological uncertainty, resulting in increased costs associated with making inappropriate behavioral decisions. The “dangerous niche” hypothesis (Greenberg and Mettke-Hofmann 2001; Mettke-Hofmann et al. 2013) posits that prey can reduce the costs associated with ecological uncertainty by increasing their level of caution or vigilance when faced with novel situations (i.e., neophobia). Higher levels of spatial and foraging neophobia would reduce costs associated with inappropriate behavioral decisions until they can acquire direct information

regarding immediate risks associated with a novel habitat or foraging opportunity (Dall et al. 2005; Mettke-Hofmann et al. 2009). For example, naïve blue tits *Parus caeruleus* and coal tits *Periparus ater* were less likely to forage on aposematic prey or conspicuously painted models than were experienced conspecifics (Exnerova et al. 2007). Likewise, migratory New World blackbirds (Icteridae) were less likely to forage on a novel food patch and spent less time in the presence of novel objects compared with resident blackbirds (Mettke-Hofmann et al. 2013). Presumably, these neophobic responses would reduce individual risks associated with uncertain situations and/or foraging opportunities.

Recently, Brown et al. (2013) expanded on the dangerous niche hypothesis, demonstrating that neophobia is an inducible, phenotypically plastic response to uncertain levels of predation risk. Using laboratory and field experiments, Brown et al. (2013) found that

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 neophobia. 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 cues), 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 $25 \times 25 \times 40$ 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 ~ 450 mL of water and added 300 mL of flake food (NutraFin). The mixture was refrigerated and allowed to set at $\sim 4^\circ$ 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 \pm SD standard length = 21.88 ± 2.18 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 cm^2 of tissue in a final volume of 430 mL. For the novel chemical cue (lemon odor), we diluted BadiaTM (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° 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 for 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 \times 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 decidedly 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

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

	<i>F</i>	<i>df</i>	<i>P</i>
Latency to enter			
Stream	8.90	2, 129	< 0.001
Stimulus	12.91	2, 129	< 0.001
Stream \times stimulus	3.10	4, 129	= 0.018
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 \times 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 \times 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 \times 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 Trinidadian guppies within each study stream

Population	<i>F</i>	<i>df</i>	<i>P</i>
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

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;

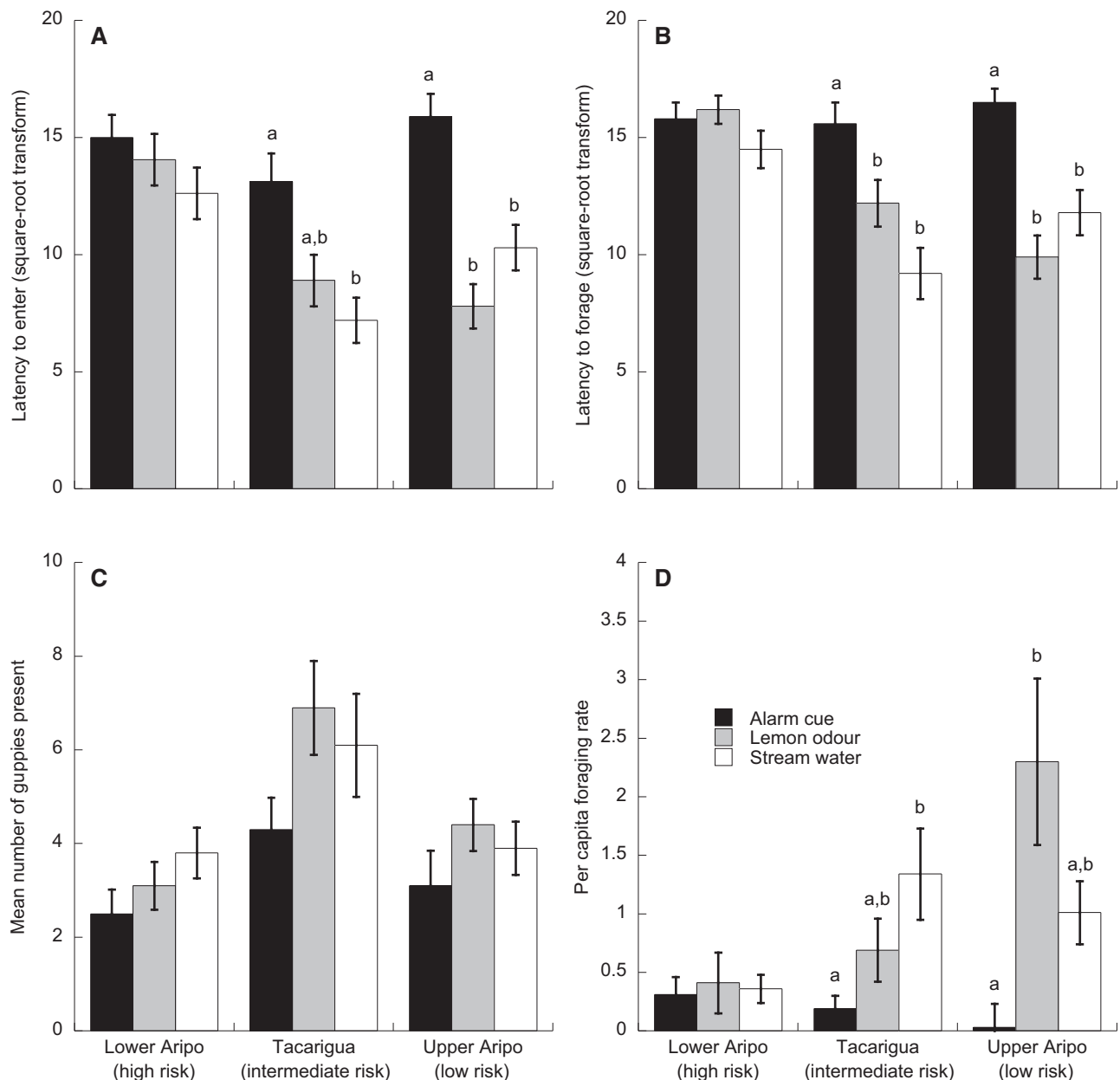


Figure 1. Mean (\pm SE) latency to enter (A), latency to forage (B), number of guppies present within 50 cm of the foraging arena (C) and per capita foraging rate (D) for guppies in the Lower Aripo (high predation), Tacarigua (intermediate predation), and Upper Aripo (low predation) Rivers. Solid bars represent conspecific alarm cues, gray bars the novel lemon odor, and open bars the stream water controls. Different letters denote significant pairwise differences ($P < 0.05$) for within-stream comparisons from Tukey's HSD.

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.

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Conflicts of interest

The authors have declared no conflicts of interest.

References

- Botham MS, Hayward RK, Morrell LJ, Croft DP, Ward JR et al., 2008. Risk-sensitive antipredator behavior in the Trinidadian guppy *Poecilia reticulata*. *Ecology* 89:3174–3185.
- Brown C, Jones F, Braithwaite V, 2005. *In situ* examination of boldness-shyness traits in the tropical poeciliid *Brachyrhaphis episcopi*. *Anim Behav* 70: 1003–1009.
- Brown GE, Chivers DP, Elvidge CK, Jackson CD, Ferrari MCO, 2014a. Background level of risk determines the intensity of predator neophobia in juvenile convict cichlids. *Behav Ecol Sociobiol* 68:127–133.
- Brown GE, Demers EE, Joyce BJ, Ferrari MCO, Chivers DP. 2015. Retention of neophobic predator recognition in juvenile convict cichlids: effects of background risk and recent experience. *Anim Cogn* 18:1331–1338.
- Brown GE, Elvidge CK, Ramnarine I, Chiver DP, Ferrari MCO, 2014b. Personality and the response to predation risk: effects of information quantity and quality. *Anim Cogn* 17:1063–1069.
- Brown GE, Elvidge CK, Ramnarine I, Ferrari MCO, Chivers DP, 2015. Background risk and recent experience influences retention of neophobic responses to predators. *Behav Ecol Sociobiol* 69:737–745.
- Brown GE, Ferrari MCO, Elvidge CK, Ramnarine I, Chivers DP, 2013. Phenotypically plastic neophobia: a response to variable predation risk. *Proc R Soc Lond B* 280:20122712–20122712.
- Brown GE, Macnaughton CJ, Elvidge CK, Ramnarine I, Godin J-GJ, 2009. Provenance and threat-sensitive predator avoidance patterns in wild-caught Trinidadian guppies. *Behav Ecol Sociobiol* 63:699–706.
- Chivers DP, Smith RJF, 1998. Chemical alarm signaling in aquatic predator-prey systems: a review and prospectus. *Écoscience* 5:338–352.
- Chivers DP, Brown GE, Ferrari MCO, 2012. The evolution of alarm substances and disturbance cues in aquatic animals. In: Brönmark C, Hansson L-A, editors. *Chemical Ecology in Aquatic Systems*. Oxford: Oxford University Press, 127–139.
- Croft DP, Botham MS, Krause J, 2004. Is sexual segregation in the guppy *Poecilia reticulata* consistent with the predation risk hypothesis? *Environ Biol Fish* 71:127–133.
- Croft DP, Morrell LJ, Wade AS, Piyapong C, Ioannou CC et al., 2006. Predation risk as a driving force for sexual segregation: a cross-opulation comparison. *Am Nat* 167:867–878.
- Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW, 2005. Information and its use by animals in evolutionary ecology. *Trends Ecol Evol* 20:187–193.
- Endler JA, Houde AE, 1995. Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution* 49:456–468.

- Elvidge CK, Brown GE, 2012. Visual and chemical prey cues as complementary predator attractants in a tropical stream fish assemblage. *Int J Zool* doi: 10.1155/2012/510920.
- Elvidge CK, Ramnarine I, Brown GE, 2014. Compensatory foraging in Trinidadian guppies: effects of acute and chronic predation threats. *Curr Zool* 60:323–332.
- Elvidge CK, Ramnarine I, Godin J-GJ, Brown GE, 2010. Size-mediated response to public cues of predation risk in a tropical stream fish. *J Fish Biol* 77:1632–1644.
- Exnerova A, Štys P, Fučíková E, Veselá S, Svádová K et al., 2007. Avoidance of aposematic prey in European tits (Paridae): learned or innate? *Behav Ecol* 18:148–156.
- Ferrari MCO, Wisenden BD, Chivers DP, 2010. Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus. *Can J Zool* 88:698–724.
- Greenberg R, Mettke-Hofmann C, 2001. Ecological aspects of neophobia and neophilia in birds. In: Nolan V, Thompson CF, editor. *Current Ornithology*. New York, NY: Springer, 119–178.
- Kelly CD, Godin J-GJ, Wright JM, 1999. Geographical variation in multiple paternity within natural populations of the guppy *Poecilia reticulata*. *Proc R Soc Lond B* 266:2403–2408.
- Kelly CD, Godin K-GJ, 2001. Predation risk reduces male-male sexual competition in the Trinidadian guppy *Poecilia reticulata*. *Behav Ecol Sociobiol* 51:95–100.
- Kelley JL, Magurran AE, 2003. Effects of relaxed predation pressure on visual predator recognition in the guppy. *Behav Ecol Sociobiol* 54:225–232.
- Lima SL, Dill LM, 1990 Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640.
- Magurran AE, 2005. *Evolutionary Ecology: The Trinidadian Guppy*. Oxford Series in Ecology and Evolution. Oxford: Oxford University Press.
- Mathot KJ, Wright J, Kempnaers B, Dingemans NJ, 2012. Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos* 121:1009–1020.
- McNamara JM, Dall SRX, 2010. Information is a fitness enhancing resource. *Oikos* 119:231–236.
- Mettke-Hofmann C, 2014. Cognitive ecology: ecological factors, life-styles, and cognition. *WIREs Cogn Sci* 5:345–360.
- Mettke-Hofmann C, Winkler H, Hamel PB, Greenberg R, 2013. Migratory New World blackbirds (icterids) are more neophobic than closely related resident icterids. *PLoS ONE* 8:e57565.
- Mettke-Hofmann C, Lorentzen S, Schlicht E, Schneider J, Werner F, 2009. Spatial neophilia and spatial neophobia in resident and migratory warblers (Sylvia). *Ethology* 115:482–492.
- Reznick D, Butler MJ IV, Rodd H, 2001. Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. *Am Nat* 157:126–140.