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Letter to Editor

Exploring the effects of anthropogenic disturbance on predator inspection activity in Trinidadian guppies

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Prey animals are often faced with uncertainty due to having imperfect information regarding current local conditions, including predation risks and the availability of reliable foraging opportunities (Dall 2010). As this uncertainty increases, the probability of making costly behavioral errors also increases, leading to more risk averse behavioral tactics (Feyten et al. 2019). For example, Trinidadian guppies *Poecilia reticulata* are far more risk averse when faced with multiple unknown sources of risk assessment information than when faced with a mix of known and unknown cues (Feyten et al. 2019). Prey can reduce uncertainty by gathering and integrating private and social information regarding current risk levels within microhabitats (Dall 2010; Munoz and Blumstein 2012). Such information acquisition can be mediated by environmental factors that affect information availability, perception, and processing of available cues (Weissburg et al. 2014). Rapid environmental changes, such as those from anthropogenic disturbances might be expected to contribute to greater ecological uncertainty experienced by prey. In Trinidad, there is a strong tradition of "river limes", in which people engage in recreational activities (e.g., picnicking, swimming, washing personal vehicles, religious ceremonies) at easily accessible locations along rivers (Deacon et al. 2015). The increased human activity associated with recreational use is known to lead to episodic turbidity, pollutants, nutrient availability, ambient noise, and habitat modifications (Deacon et al. 2015 and references therein). These anthropogenic disturbances could lead to increased uncertainty, either by reducing the availability of information or by reducing the reliability of information regarding current conditions. For example, increased turbidity might restrict visual information, while detergents (from bathing or dishwashing) may temporarily disrupt the detection of chemosensory risk cues. Such unpredictable disturbances would reduce information availability within a microhabitat patch, reducing the ability of prey to assess current conditions. Alternatively, cues can be considered reliable if they consistently indicate "risky" vs. "safe" conditions (Feyten et al. 2021). Localized disturbances may reduce the probability that a cue indicates a specific outcome (i.e. indicates potential predation risk vs. potential foraging opportunity). Either (or a combination) of these mechanisms would be expected to increase the degree of uncertainty of risk among prey. Crucially, these disturbed sites are typically in close proximity to relatively unused stretches of the river, allowing for ready comparisons between "disturbed" and "undisturbed" sites (Deacon et al. 2015), and testing hypotheses regarding the impact of uncertainty in information availability to prey. Here, we hypothesized that increased uncertainty of risk resulting from anthropogenic (recreational) disturbances should increase the need of guppies to gather information regarding the identity and level of local predation threats.

Using *in-situ* observations, we explored the impact of localized anthropogenic disturbance on the predator inspection behavior among Trinidadian guppies *Poecilia reticulata*. Predator inspection behavior, in which prey make saltatory approaches towards a predator, allows prey to gain information regarding the identity and risk of potential predators and even learn to recognize novel predators (Brown and Godin 1999). If recreational disturbance leads to more uncertainty, inspection activity may be higher in disturbed locations, relative to paired undisturbed (upstream) locations. However, approaching a potential predator, particularly an unknown predator, is also risky (Brown and Godin 1999). Our initial prediction is that guppies tested in higher predation risk populations should exhibit lower inspection activity. Our second prediction is that if disturbances result in only an increase in uncertainty of risk, we should expect a decrease in inspection activity due to elevated costs of predation. Conversely, as disturbances may indicate the presence of both risk *and* reward, guppies may increase inspection activity to compensate for reduced reliability of information within disturbed vs. undisturbed sites. We conducted *in situ* observations within and above known recreational sites ($n = 4$) on two rivers within the Northern Range Mountains, Republic of Trinidad and Tobago (Supplementary Material). The sites vary in ambient predation pressure from low (Upper Aripo River) to very high (Lower Aripo River; Deacon et al. 2018). One of the sites on the Lopinot River (Lopinot A) has high predation pressure, similar to the Lower Aripo River, while the other Lopinot site

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(Lopinot B) has lower predator diversity and abundance (personal observations). We quantified the latency to inspect, inspection rate, and inspecting group size towards a novel predator model over a four-minute observation period (n = 10 per sampling location). Using a principal components analysis, we calculated predator inspection activity scores as a dependent variable (see Supplemental information for details). A General Linear Mixed Model revealed a significant main effect of disturbance, where inspection activity was significantly higher within the disturbed locations, relative to those immediately upstream ($F_{1, 3.001}$ = 57.45, P = 0.005; Figure 1), across all rivers. There was also a main effect of river ($F_{3,3}$ = 21.01, P = 0.016), with the highest level of inspection activity seen in the low predation risk stream (Upper Aripo; Figure 1). Finally, there was no interaction between site and river ($F_{3,68}$ = 0.43, P = 0.74; Figure 1). It is unlikely that these effects are due to local densities of guppies, as catch per seine haul (Supplementary Table S1) was lower in the recreational sites as well as in the lower predation rivers (i.e., highest inspection activity in sites with lower densities of guppies). These results are supportive of the hypothesis that exposure to anthropogenic disturbance increases uncertainty for guppies and that they may compensate for this uncertainty with increased reliance on information acquisition.

Failing to respond appropriately to relevant predation threats brings dramatic increases in the risk of mortality (Elvidge and Brown 2014). However, responding to irrelevant "threats" can result in decreased opportunities to forage, court, and/or mate (Brown et al. 2013). As uncertainty increases, these "lost opportunity" costs are also likely to increase. As a result, the increased inspection activity observed at disturbed locations should benefit guppies by allowing them to rapidly reduce the costs associated with decreased or unpredictable information availability regarding predation threats. Increased inspection activity would allow prey to better manage the conflicting demands of detecting and avoiding predators while still maintaining time and energy for other activities such as foraging and mating (Brown and Godin 1999). Interestingly, we found the highest overall inspection activity scores within the Upper Aripo River (lowest predation pressures), consistent with previous reports suggesting that high ambient predation risk leads to more risk averse inspection patterns (Brown et al. 2013). More importantly, we observed the same pattern of inspection activity across all four sites, with higher levels within disturbed sites relative to undisturbed sites. Human activities may simply reduce predation risk within disturbed sites leading to an increase in inspection activity. However, Deacon et al. (2015) reported that predator density was not impacted by human recreational disturbance, suggesting that localized reductions in predation risk might not be a driving factor. Given that recreational use likely results in unpredictably episodic increases in disturbance (i.e. turbidity, nutrient availability, predator movements), we posit that human activities may increase the variance of predator activity, hence increasing uncertainty of risk and/or rewards experienced by prey. Alternatively, human recreational activity may alter the perception of risk among prey populations. Above recreational sites, novelty would be more likely to be a consistent indicator of risk and prey should exhibit lower levels of inspection activity (Brown et al. 2013). However, within areas of high human activity, novelty may also be consistent indicators of potential foraging opportunities (mixing of substrate; food wastes from dish washing). As a result, within disturbed sites, novelty may be inconsistently associated with risk and/or reward, further leading to increased uncertainty but different cost-benefit tradeoffs of gathering information compared to undisturbed sites. Thus, our results are consistent with the hypothesis that increases in uncertainty of risk and reward are important factors in driving the risk assessment patterns of guppies. An intriguing possibility is that elevated human activity may result in prey making learned associations between novelty and safety. Such associations would potentially leave prey at greater vulnerability to novel predation threats. While our current observations do not allow us to draw conclusions regarding the precise ecological mechanism at play, they do highlight the need for additional research. Predicting how individual or suites of anthropogenic disruptions alter risk assessment information is a pressing question for ecologists. Clearly, while additional research is needed, our results point to an exciting opportunity to explore the drivers of ecological uncertainty and the behavioral and cognitive responses to this uncertainty under fully natural conditions.

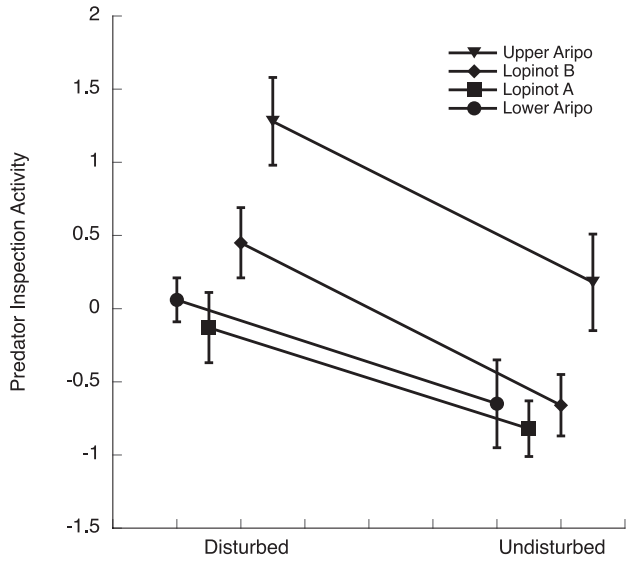

Figure 1: Mean (± SE) predator inspection activity scores of guppies at disturbed (recreational) and undisturbed (above) sites. Higher activity scores represent shorter latency to initial inspection, higher inspection rates, and larger inspecting group sizes; lower activity scores represent longer latency to initial inspection, lower inspection rates, and smaller inspecting group sizes.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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