Letter to the Editor

Predation risk assessment based on uncertain information: interacting effects of known and unknown cues

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Handling editor: Jian-Xu Zhang

Received on 27 June 2018; accepted on 8 November 2018

Prey use reliable public information in order to assess local habitat conditions such as predation risks, competitive interactions, and foraging opportunities (Dall et al. 2005), allowing for context appropriate behavioral decisions. However, public information can often differ widely in reliability (Feyten and Brown 2018), increasing the potential costs associated with behavioral decision making (Dall et al. 2005). The reliability of public information is expected to decrease with increased uncertainty of environmental conditions (Koops 2004; Dall et al. 2005), where ecological uncertainty is the ambiguity about the current state of the environment due to imperfect or incomplete information (Dall et al. 2005; Munoz and Blumstein 2012; Feyten and Brown 2018). Consequently, prey have at their disposal a variety of sources of public information, ranging from known or reliable (e.g., genetically fixed conspecific alarm cues; learned predator cues) to unknown or unreliable (e.g., neophobic responses to novel cues; Ferrari et al. 2007; Brown et al. 2013; Feyten and Brown 2018). The effect of ecological uncertainty, and the resulting reliability of information, becomes increasingly complex when we consider that prey integrate information from multiple sources in order to make behavioral decisions (i.e., sensory complementarity; Lima and Steury 2005; Munoz and Blumstein 2012).

Error management theory (Johnson et al. 2013) predicts that as risks become more uncertain (i.e., higher proportion of unknown vs. known information), prey should shift to a more risk-averse tactic (i.e., become more cautious). Thus, we predict that when prey face multiple unreliable (i.e., unknown) cues, they should "overestimate" risk compared with when they faced cues of mixed reliability. To test this question, we conducted *in situ* predator inspection trials, which are a well-established estimate of perceived predation risk (Brown et al. 2013). We paired known and unknown visual riskassessment cues (predator models) with a known, unknown, and control chemosensory risk-assessment cues (alarm cue, lemon odor, and stream water, respectively; see Supplementary Materials). We found that the number of guppies present was not influenced by predator models ($F_{1.72} = 3.36$, P=0.07), chemosensory cues $(F_{2,72} = 1.80, P = 0.17)$, or the interaction of predator models and chemosensory cues ($F_{2,72} = 0.21$, P=0.81, Figure 1A), allowing us to directly compare latency to inspect as a measure of "perceived predation risk." We found that the mean latency to inspect was shaped by both the predator model and chemosensory cue (interaction: $F_{2,72} = 9.44$, P < 0.001), as well as by the chemosensory cue alone $(F_{2,72} = 30.37, P < 0.001)$, but not by predator model alone ($F_{1.72} = 2.49$, P=0.12, Figure 1B). Post hoc *t*-tests demonstrate that the latency to inspect was significantly longer when a novel chemosensory cue was paired with a novel predator model, compared with when it was paired with a known predator model (t = -4.12, df = 22, P<0.001, Figure 1B). However, the latency to inspect did not differ between the known versus novel predator models when paired with a known chemosensory cue (t = 1.42, df = 22, df = 22)P = 0.17) or a stream water control (t = -0.63, df = 22, P = 0.54). When prey are faced with cues of mixed reliability, they appear to rely on the known cue to assess the level of acute threat (the known cue is dominant; Munoz and Blumstein 2012). However, guppies exhibited the highest level of perceived predation risk when exposed to two unknown sources of information, compared with when at least one source of information was known (i.e., reliable). We suggest that in the absence of at least one source of known (i.e., reliable) information, there are additive effects of sensory complementarity (i.e., enhancement of redundant information; Munoz and Blumstein 2012), such that guppies "overestimate" the level of perceived predation risk.

Having a combination of genetically fixed, learned, and neophobic responses may allow prey to minimize costs while making optimal

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Figure 1. Mean (\pm *SE*) number of guppies present (**A**) and latency to inspect (**B**) the known or novel visual cues (predator models) paired with known (alarm cue; gray bars), unknown (lemon odor; striped bars), or control (stream water; white bars) chemosensory cues. An increase in latency to inspect is consistent with increased perceived predation risk (Brown et al. 2013). *N* = 12 per treatment combination.

decisions in the face of predation risk. For example, learning can be costly since prey must survive initial predator encounters (Ferrari et al. 2007; Brown et al. 2013), use energy and time which might otherwise be invested in other fitness activities (Dall et al. 2005), and potentially face unknown (i.e., unreliable) cues before they can gain experience and learn how to respond. Meanwhile, neophobic responses can be costly when the missed opportunities of engaging in other fitness-related activities accrue. Indeed, if neither the reliable nor

unreliable cue conveys an actual threat, the neophobic response to these cues will diminish in a process akin to latent inhibition. Similarly, if prey are faced with two unknown cues which do not entail risk, we expect neophobic predator avoidance responses to fade. However, background levels of risk influence how quickly the response is inhibited (Brown et al. 2015). Taken together, we propose that prey can respond to a combination of unreliable "unknown" and reliable known sources of information by using genetically fixed responses, learning, and neophobia. Furthermore, prey can integrate this diversity of information sources in order to optimize behavioral decision making.

Acknowledgments

The authors specially thanks Kharran Deonarinesingh for invaluable assistance in the laboratory and field.

Funding

This work was financially supported by the Natural Science and Engineering Research Council of Canada Discovery Grants program to G.E.B. and the Faculty of Arts and Science Graduate Support to L.E.A.F. and E.E.M.D.

Supplementary Material

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

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