



Living on the edge: how does environmental risk affect the behavioural and cognitive ecology of prey?



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Prey show remarkable plasticity across a range of traits that allow them to adapt to changes in predation risk in their local environment. While we know much about behavioural, morphological, physiological and life-history responses, we know less about how background risk alters cognitive functioning related to risk assessment. Here, we exposed wood frog tadpoles, *Lithobates sylvaticus*, to high- or low-risk environments for 7 days. Following this, we exposed tadpoles to one of four treatments that either continued risk, ended risk, taught tadpoles to recognize a predator or provided a false predator learning control. Tadpoles were tested for responses to predator odour, alarm cues or water either 1 day or 11 days after conditioning ended. Comparisons between conditioning treatments and test odours allowed us to assess how background risk alters a range of cognitive functions relating to risk assessment. Tadpoles that experienced high background risk responded to alarm cues with a weaker response than low-risk tadpoles, as predicted by the risk allocation hypothesis. High-risk tadpoles also developed neophobic responses to novel odours, unlike low-risk tadpoles, but displayed similar responses to a learned predator as tadpoles from low risk. When tested again 11 days later, high- and low-risk tadpoles responded equally across all treatments with the exception of learned predator responses, where high-risk tadpoles still responded strongly to the predator odour, while low-risk tadpoles did not. Our results demonstrate that recent experience with risk induces short-term cognitive plasticity in a number of functions related to risk assessment.

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Living with predators has resulted in the development of a diverse array of antipredator responses that reduce the chances of being eaten. Such responses include alterations to life-history strategies (Benard, 2004; Crowl & Covich, 1990; DeWitt, 1998), morphology (Brönmark & Miner, 1992; DeWitt, 1998; Relyea, 2004) and behavioural adaptations (Brown, Ferrari, Elvidge, Ramnarine, & Chivers, 2013; Lima, 1998; Miner, Sultan, Morgan, Padilla, & Relyea, 2005). However, maintaining these responses results in lost opportunities and reduced growth or fecundity; thus, maintenance of antipredator responses is costly (Lima & Dill, 1990). While certain traits vary in response to interactions with predators over evolutionary timescales, others such as behaviour are more plastic, allowing prey to respond to predators over multiple temporal scales and minimize the costs associated with antipredator responses (Kelley & Magurran, 2003; Lima & Bednekoff, 1999). These

responses are often influenced by prior experience with risk at both the individual and population level (Brown, Rive, Ferrari, & Chivers, 2006; Deecke, Slater, & Ford, 2002; Lima & Bednekoff, 1999).

At the cognitive level (incorporating mechanisms of perception, learning, memory and decision making; Shettleworth, 2010), performance is strongly related to the environmental characteristics that prey experience, including predation risk (Abrahamse, Lubbe, Verwey, Szumska, & Jaskowski, 2012; Brown & Braithwaite, 2005; Buchanan, Grindstaff, & Pravosudov, 2013). For example, poeciliids from a high-risk population were slower to solve a foraging task (Brown & Braithwaite, 2005) and made more mistakes during a sequential learning task (Beri, Patton, & Braithwaite, 2014). More recently, Brown et al. (2013) showed that cognitive function can be highly plastic in response to recent experience with predation risk. They demonstrated that both fish and larval amphibians maintained in a low-risk environment for 7 days did not respond to odours of a novel predator. However, individuals maintained in a high-risk environment displayed a strong neophobic response to the same novel cues. This environmentally induced neophobia acts

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across sensory systems (Meuthen, Baldauf, Bakker, & Thünken, 2015) and was hypothesized to reduce the costs of learning when exposed to uncertain, risky environments (Brown et al., 2013). Further studies have revealed that short-term increases in background risk also influence how prey learn about predators and nonpredators (Chivers, McCormick, Mitchell, Ramasamy, & Ferrari, 2014; Ferrari, 2014). Such results suggest that short-term alterations in risk levels experienced by prey may significantly alter performance across a range of cognitive functions related to risk perception.

The temporal variation in predation risk means that while changes to antipredator responses, as discussed above, may be optimal during periods of high risk, they may be suboptimal during periods of low risk as they reduce time available for other fitness-enhancing activities. We have a clear understanding of how investment in antipredator responses is shaped by temporal variation in predation risk in the context of the risk allocation hypothesis (Ferrari, Sih, & Chivers, 2009; Lima & Bednekoff, 1999; Sih, Ziemba, & Harding, 2000), yet we know little about how long these high-risk-induced traits last following the transition from a period of high risk to low risk or the factors that might influence the rate of change between states. Learned responses to predators are dependent on the context in which they are first encountered, with the level of risk and certainty about the predator determining how prey respond during future encounters (Ferrari, Brown, Bortolotti, & Chivers, 2010; Mitchell & McCormick, 2013). Thus, we might expect neophobic responses to novel predators to diminish faster than learned responses to predators, if a lack of direct association with risk leads to a lower level of perceived risk or certainty about the novel predator's identity. Similarly, learned responses in high-risk environments may be greater and retained for longer compared to those learned in low-risk environments if the background risk acts in an additive or synergistic manner with the risk during the conditioning event.

While population-level differences in performance of cognitive abilities have been demonstrated to result from different levels of predation (Brown & Braithwaite, 2005; Brydges, Heathcote, & Braithwaite, 2008), we know little about the short-term consequences of variable risk on the plasticity of prey cognition or the potential carryover effects once risk levels abate. Our goal was to test how background risk alters behavioural responses across a range of cognitive functions relating to the assessment of predation risk. To do this, we used a classic model system for understanding phenotypic plasticity: larval amphibians. Larval amphibians are known to be highly responsive to predation cues and show remarkable morphological plasticity following their detection (Relyea, 2001, 2003). Brown et al. (2013) recently demonstrated that this plasticity extends to cognitive function, as high background risk induced a neophobic response, but whether this plasticity extends to other cognitive functions or is reversible remains unknown. We maintained woodfrog tadpoles, *Lithobates sylvaticus*, in a high- or low-risk environment for 7 days by exposing them to chemical cues from injured conspecifics (hereafter 'alarm cues'). Alarm cues are used by a wide variety of species, provide reliable information about local predation risk and are innately recognized by anuran tadpoles (Ferrari, Brown, et al., 2010; Ferrari, Chivers, & Wisenden, 2010; Schoeppner & Relyea, 2009). Following the end of this background risk period, we exposed tadpoles to one of four different treatments: (1) continued risk (alarm cues + water), (2) learned predator conditioning (alarm cues + tiger salamander odour (*Ambystoma tigrinum*); a novel predator), (3) false learned predator conditioning (water + salamander odour) or (4) a control (water + water). The two cues in each of the above four treatments were added separately so as to control for the disturbance effects of adding the cues. The next day, we tested tadpoles from all

conditioning groups for their response to one of the three cues (water, salamander odour or alarm cues). The specific odour combinations used here represent a variation of the classical Pavlovian conditioning protocol and relevant controls, where presenting an unconditioned stimulus (novel predator odour) with a conditioned stimulus (alarm cues) labels the unconditioned stimulus as a risk (Suboski, 1990). In subsequent encounters with the previously unconditioned stimulus the individuals display a response similar to the paired conditioned stimulus. Behavioural responses to cues following the various conditionings allowed us to test how background levels of risk affect a range of cognitive functions, including general responses to predation risk cues, responses to novel odours, the short-term effect of experience with novel odours and learned responses to predators. Additionally, to test the relatively long-term effects of background risk, we tested all groups again after 11 days of low risk.

METHODS

Experimental Overview

The design first consisted of exposing tadpoles to a low or high background level of risk for 7 days. Once the background risk was established, the tadpoles were conditioned to one of four treatments: water only (W + W), alarm cues only (AC + W), predator odour only (W + PO) or alarm cues paired with predator odour (AC + PO). The tadpoles were subsequently tested, either 1 day or 11 days later, for their response to one of three cues: water (disturbance, negative control), predator odour or alarm cues (positive control).

Experimental Protocol

The experiment took place outdoors, under natural light (16:8 h light:dark cycle), temperature (range 10–26 °C) and weather conditions, during May and June 2012. Six woodfrog egg clutches were collected the day after being laid, from a pond at our field site near Sherwood Park, Alberta, Canada. They were placed in two pools (1.2 × 0.6 m; diameter × depth) filled with well water and positioned floating on the pond so as to equalize the temperature of the pools with that of the pond. Slough grass and dead leaf matter were added to the pools to provide food and shelter to the newly hatched tadpoles. The clutches were left undisturbed until hatching (~5 days), after which we added alfalfa pellets (food) every 2 days to the pools, to complement the algae growing in the pool. The tadpoles were left to grow for 2 weeks, after which time they were ready to be used in our experiment (Gosner stage 25).

We set up 80 3.7-litre pails filled with well water. In each pail, we placed 15 tadpoles, randomly selected from the two pools. Each of the 80 pails was then randomly allocated to one of two risk treatments (high risk versus low risk). The pails were positioned under the trees bordering the pond for shade, to avoid stressful heating events from sun exposure. Following the methodology of Brown et al. (2013), we manipulated background risk by exposing tadpoles to either 20 ml of well water (low risk) or 20 ml of alarm cue solution (high risk) twice a day for 7 consecutive days. Previous studies have shown that prey animals, including tadpoles, generally cue in to the temporal pattern of risk in their environment after 3 days (Ferrari et al., 2009). To prepare the alarm cue solution, tadpoles were placed in a mortar and euthanized with a rapid blow to the head (using a pestle). Three tadpoles were completely pulverized in a few seconds (euthanasia protocols were carried out in accordance with the University Committee on Animal Care and Supply Protocol 20060014). After this, we added 20 ml of well water. Care was taken to select tadpoles of a similar size throughout

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