



Short-term environmental variation in predation risk leads to differential performance in predation-related cognitive function



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Predation produces strong selection on numerous traits affecting prey survival, such as morphology or behaviour. However, little is known about the influence of predation on behavioural traits that reflect cognitive abilities. Two studies have shown negative relationships between predation pressure and performance in foraging-related tasks in different populations of fish. Whether these differences are due to population differences or plasticity is unknown. In addition, little is known of the effect of predation risk on predator-related cognitive function. Here, I exposed woodfrog, *Lithobates sylvaticus*, tadpoles to a high or low level of background risk using injured conspecific cues for 4 days. Following this period, I conditioned them to recognize a novel predator as a threat. I compared the intensity of the learned response between the two groups the following day, and compared retention after 10 days. I found that high-risk tadpoles learned to respond to the predator with a greater intensity of antipredator response and retained the response longer compared to low-risk tadpoles. This is the first study to demonstrate that recent history of predation risk can affect the cognition of prey, demonstrating plasticity in a relatively fixed learning mechanism. My results also raise questions regarding the existence of cross-contextual cognitive trade-offs in animals: increased cognition in predation-related tasks may come at the expense of foraging-related tasks.

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Predation produces strong selection affecting the lives of prey animals, and its consequences are visible at all ecological scales, from changes in short-term behavioural decisions (Lima & Dill, 1990) to changes in community structure and ecosystem functioning (Ives, Cardinale, & Snyder, 2005). In addition to the obvious consumptive effects of predators, myriad changes are seen simply as a response to the presence of predators. These effects, stemming from predator intimidation or trait-mediated indirect interactions, have been shown to cause most of the predation-related changes seen at all ecological scales (Preisser, Bolnick, & Benard, 2005). These changes are mediated through alterations at the individual level. Predators can cause changes in prey morphology, leading to the evolution of either constitutive or inducible defences (Gotthard & Nylin, 1995). To decrease predation risk, prey also show plasticity in the timing of crucial life-history traits, such as the timing of hatching or metamorphosis (Benard, 2004; Chivers et al., 2001). These changes are often the result of long evolutionary exposure to predators and are often expressed in response to predator-specific

threats. Among the most plastic traits, behavioural alterations in response to predation have been widely described in numerous contexts. Most mobile prey have many options and can reduce their chances of encountering a predator by altering where and when they forage, what they eat and with whom they mate (Lima, 1998). Upon encountering a predator, they can also reduce their likelihood of being captured by dashing and reaching shelter or freezing and adopting cryptic postures. The presence of predators can thus have profound effects of all aspects of an individual's life.

One well-studied aspect of prey's lives is their ability to learn about risk and subsequently alter their behaviour to increase survival (Brown & Chivers, 2005; Brown & Laland, 2003). In fact, all the behavioural alterations described above rest on the basic tenet that prey have to recognize predators before they can respond to them adaptively. Given the direct survival benefits resulting from learning potential predators among the myriad species in the community, it is not surprising that prey show highly effective and varied learning mechanisms. Whether the learning results from direct experience, social learning from observing conspecifics (Crane & Ferrari, 2013) or via alarm calls or injured conspecific cues, one 'training' session is usually enough to cause changes in behaviour and the labelling of the predator as a threat (Ferrari, Wisenden, & Chivers, 2010).

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It is well known that environmental and ecological constraints shape the cognitive ecology of animals. Species with different foraging tactics will differ in the way food-related information is processed. Food-caching species, for instance, possess better spatial memory than noncaching species (Shettleworth, 1990). Species living in complex habitats are better at solving spatial tasks such as mazes (Williams et al., 2001). Cognitive abilities can also vary throughout an individual's life, such as adaptive ontogenetic changes in cognitive performance associated with changes in habitat types (Takahashi, Masuda, & Yamashita, 2010). The potential for those cognitive traits to change according to environmental variation is known as cognitive plasticity. When it comes to the effect of predation on cognitive plasticity, a handful of studies have demonstrated differences in spatial-learning tasks between populations of fish. Brown and Braithwaite (2005) showed that poeciliids from low-predation/low-competition populations solved a maze faster than those from high-risk/high-competition populations. Similarly, Brydges, Heathcote, and Braithwaite (2008) found that sticklebacks (*Gasterosteus aculeatus*) from low-predation populations learned a foraging task faster and retained the information longer than fish from the high-predation populations. These results suggest that differences in environmental conditions between the populations may drive some phenotypic plasticity in cognitive traits. Specifically, the presence of predation-related stressors might lead to poorer performance in the cognitive tasks. Whether such cognitive plasticity reflects selection-mediated, population-level differences or individual plasticity is unknown. If the presence of predators can act as a stressor and in turn lead to poorer predation-related cognitive function, it could provide a negative feedback loop that would render prey living in predation-rich environments more susceptible to predation, by decreasing the amount of learning-mediated antipredator adaptations observed in the community.

My goal in this study was to investigate the effect of short-term exposure to predation on predation-related cognitive traits, namely learning and retention of predator information, and to assess the existence of individual cognitive plasticity. A recent study by Brown, Ferrari, Elvidge, Ramnarine, and Chivers (2013) showed that short-term exposure to predation risk could lead to dramatic changes in responses to novel stimuli. Fish and larval amphibians maintained in a high-risk environment for 4 days showed neophobic (fear of anything new) responses to novel odours, while those maintained in a low-risk environment did not respond to those unknown stimuli. Predation risk is therefore causing deep alteration in the way in which prey interpret what is risky, and this, in turn, could likely affect how risk-related information is learned and/or retained. I maintained woodfrog tadpoles, *Lithobates sylvaticus*, in a high-risk or low-risk environment using injured conspecific cues. In aquatic ecosystems, freshwater and marine alike, a wide diversity of prey, ranging from corals to amphibians, respond to injured conspecific cues with immediate antipredator responses, which in turn, gives them a survival advantage during predator–prey encounters (Chivers et al., 2013; Ferrari, Wisenden, et al., 2010). Using these cues to create a risky environment is advantageous as it does not provide prey with a predator-specific context, and hence, does not bias the learning of one type of predator over another. Following this risk exposure period, I conditioned the tadpoles from both groups to recognize a novel tiger salamander, *Ambystoma tigrinum*, as a predator via pairing of injured conspecific cues with salamander odour. This is a well-established learning paradigm in many aquatic species, including woodfrogs (Ferrari & Chivers, 2009). The tadpoles were then tested for their response to salamander odour alone or to a water control, either the next day or 10 days later. I compared the occurrence and intensity of the learned response to the predator 1 day

postconditioning, and again after 10 days. If predation risk is acting as a negative stressor, I predicted that high-risk tadpoles would learn to respond to the predator with a lower intensity and lose their response quicker. However, if the high-risk conditions provide a stimulating environment leading to risk-averse cognitive traits (as seen with the neophobic responses), I expected high-risk prey to learn to associate the predator with higher threat and maintain a stronger response for longer.

METHODS

Ethical Note

All work performed herein was approved by the University of Saskatchewan Animal Care protocol 20060014.

All procedures took place outdoors, allowing tadpoles to experience natural conditions (temperature, precipitation, sun exposure) and other factors that may vary naturally in the field. Four weeks prior to starting the experiment, a 1900-litre tub was filled with well-water and seeded with plankton and aquatic plants (sedges, slough grasses) from a local pond. This procedure ensured that the water that would be used in the experiment contained natural pond odours, but lacked any cues from potential predators. Tadpoles were collected as eggs (six egg masses) in nearby ponds and raised in separate pools to control for food availability and predation pressure. Tadpoles fed on algae present in the pool, along with a supplement of alfalfa chow. The salamanders were originally collected from a Saskatchewan pond and maintained in the laboratory for 3 years. They were fed earthworms, every 3 days for 2 weeks, prior to use in the experiment.

Experimental Design

Background risk

Groups of 12 tadpoles were placed in each of 36 pails containing 2 litres of water. The 36 pails were randomly allocated to one of four groups resulting from the following 2×2 design: tadpoles would experience either a low or high background level of risk for 4 days, and would then undergo either a pseudoconditioning (water paired with salamander odour: no learning) or a true conditioning (injured conspecific cues paired with salamander odour: learning). High- and low-risk conditions followed established protocols (Brown et al., 2013). Tadpoles in the high-risk group received an injection of injured conspecific cues three times/day for 4 days, while those in the low-risk group received a water injection on the same schedule. The injection of injured conspecific cues was obtained by placing three tadpoles in a mortar, quickly removing excess water and euthanizing them with a blow to the head using the pestle (Ferrari & Chivers, 2009). The bodies of the tadpoles were then grinded to a paste, which was then suspended in 10 ml of water. This solution was filtered and then injected in one of the pails. The injections were distributed throughout the day, from 0900 until 1800 h, with at least a 3 h delay between injections. Each pail contained an excess of alfalfa pellets to ensure that food was always available to the tadpoles. The water in each pail was changed once daily, 1 h after the last injection of the day, and food was added immediately after the water change.

Conditioning

The day following the end of the 4-day exposure, half of the pails in the high-risk and low-risk treatments received a conditioning of 10 ml of injured conspecific cues and 20 ml of salamander odour, while the other pails received a pseudoconditioning of 10 ml of water paired with 20 ml of salamander odour. Once again, the water was changed 1 h after the end of the conditioning procedure

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