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Understanding the role of uncertainty on learning and retention of predator information

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Abstract Due to the highly variable nature of predation risk, prey animals need to continuously collect information regarding the risk posed by predators. One question that ensues is how long to use this information for? An adaptive framework of predator-related information use predicted that certainty should influence the duration for which information regarding the threatening nature of a species is used in decision-making. It predicts that uncertainty contributes to the reduction in the duration of information use, due to the cost of displaying antipredator behaviours towards non-threatening species. Here, we test this prediction using repetition of conditioning events as a way to increase the certainty associated with the predatory nature of a novel salamander for woodfrog tadpoles. Tadpoles were conditioned 1, 2 or 4 times to recognize a novel salamander as a predator and subsequently tested for their response to the salamander 1 day or 11 days post-conditioning. We found that conditioning repetition did not affect the intensity with which tadpoles learned to respond to the salamander after 1 day. However, after 11 days, tadpoles with fewer conditionings responded to the salamander with a weaker intensity than those that received more conditionings. Our results provide support for the model prediction that an increase in the certainty associated with correctly identifying a predator leads to longer retention of the threat.

Keywords Uncertainty · Information use · Learned predator recognition · Memory · Woodfrog *Rana sylvatica* · Retention · Learning · Antipredator behaviour

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Introduction

Predation risk is highly variable both in space and in time (Lima and Dill 1990; Ferrari et al. 2009b). Thus, to optimize their allocation of energy and time among different activities, prey animals need to adjust the intensity of their antipredator response according to ambient levels of risk (Helfman 1989; Puttlitz et al. 1999). To accomplish this, prey animals continually integrate information they collect about predators and non-predators, to match current risk conditions. While the field of behavioural ecology is ripe with experiments that attempt to understand how animals learn to recognize predators as dangerous (Mathis et al. 2003; Griffin 2004; Wisenden et al. 2004; Brown and Chivers 2005), much less attention has been given to understanding how long such information should be retained by prey animals (Ferrari et al. 2010a; Brown et al. 2011). Are there situations where information should be retained for short periods of time and others where the retention should be longer? In other words, how long does a piece of information retain its value, and consequently, how long should it be used in the complex decision-making algorithm used by animals?

A number of theoretical papers have attempted to investigate the functionalities of forgetting. Going away from the assumption that forgetting was a 'bad' thing, a

mere failure of the brain, scientists have started to investigate it in the context of 'adaptive forgetting', whereby getting rid of old information was necessary to maintain accurate decision-making in a variable environment, thus making it an adaptive mechanism (Bouton 1994; Kraemer and Golding 1997). Some have modelled the information retention period (or memory window) as a fixed parameter, and for which all information collected within this timeframe are contributing equally to the decision-making process, while older information is ignored (Killeen 1981; McNamara and Houston 1987). In contrast, some have modelled a memory window, for which information is weighted in a manner proportional to their recentness (McNamara and Houston 1987; Devenport and Devenport 1994). Others have maintained the variance-related exponential weighting, but have added a parameter of memory devaluation that simply adds flexibility to memory window, which can become longer or shorter based on the profitability and accuracy of the information it contains (Hirvonen et al. 1999; Dunlap et al. 2009). All the aforementioned work has been done in the context of foraging-related information, and little has been done to understand similar patterns of information use in a predation context (Ferrari et al. 2010a). Some factors affecting the acquisition and retention of food-related information may also affect the acquisition and retention of predator-related information. However, the marked difference in the cost-benefit matrix associated with errors or wrong use of information (life-dinner principle) results in differences in the direction and value of contribution of these factors. Thus, predation deserves a clear framework of information use adapted to the cost-benefit trade-offs that are unique to predator–prey interactions. Ferrari et al. (2010a) were the first to develop a comprehensive model for the memory associated with learned predator recognition. They argue that a number of intrinsic and extrinsic factors influence the duration for which prey should remember predators. One such intrinsic factor is the certainty associated with correctly identifying the predator as a threat. The more certain the prey is that the predator is in fact a predator, the longer the retention should be, i.e. the longer the piece of information relating to this predator should contribute to the decision-making.

In this paper, we explore the dynamics of predator learning and memory using woodfrog tadpoles (*Rana sylvatica*) as a test species. Like many aquatic prey species, tadpoles learn to recognize potential predators when they detect cues from injured conspecifics at the same time as they detect an unknown stimulus such as the odour of a novel predator (Mirza et al. 2006; Ferrari et al. 2008; Gonzalo et al. 2009). This learning is highly effective and often requires only a single conditioning event for the information to be learned. However, the paradox of such

highly efficient learning is that prey may inadvertently learn to recognize a non-predator as dangerous if it happens to be in the vicinity when the prey detects injured conspecific cues. Obviously, prey cannot be 100 % certain that an animal that happens to be associated with injured conspecific cues is in fact a predator. If prey can increase their certainty that the unknown animal is indeed a predator, then the memory associated with that animal should be longer (Ferrari et al. 2010a).

The only experiment to indirectly test whether the level of certainty influences the memory of predators was conducted by Ferrari et al. (2010a). They exposed woodfrog tadpoles to alarm cues paired with the odour of tiger salamanders (*Ambystoma tigrinum*) and then subsequently tested the tadpoles for responses to both salamanders and newts (*Cynops pyrrhogaster*), which have never been encountered before. The tadpoles responded to the salamanders and generalized their predator recognition to the newts. However, the length of the memory window was shorter for the newt than for the salamander. Ferrari et al. (2010a) argue that this likely reflects differences in certainty associated with whether newt and salamanders are indeed predators. Given that the tadpoles had to generalize (or extrapolate) their recognition to the newt, there was less certainty that the newt was indeed a predator. However, the results could also reflect differential retention based on response intensity, whereby information regarding higher threats (salamander) was retained longer than lower threat (newt). In this study, we apply a direct test of whether the level of certainty influences predator learning. We exposed tadpoles to injured conspecific cues paired with the odour of a salamander (conditioned learning) 1, 2 or 4 times and then tested for retention of the predator odour as a threat. We argue that as the number of conditionings increases, the certainty that the salamander is indeed a predator also increases, which should lead to a longer retention of the information by the tadpoles.

Methods

Field site and test subjects

Our field site is located in central Alberta, Canada. Woodfrogs are explosive breeders, and at our location, adults breed over a period of approximately 2 weeks in late April and early May. Our previous work has demonstrated that woodfrogs from this population do not show anti-predator response to salamander cues without any experience (Ferrari et al. 2007; Ferrari and Chivers 2009). Four weeks prior to the start of the experiment, a 6,000-L outdoor pool was filled with well water and seeded with plankton and aquatic plants from a local pond. This

ensured that our test water did not contain any cues from predatory salamanders, but contained a range of natural pond odours.

Eight freshly laid woodfrog egg clutches were collected from a local pond and placed in a pool containing well water and plants from the pond. Plants were added to provide an algal source to the pool. The pool was placed on the pond, floating, to ensure that the temperature and sun exposure of the pool were the same as those of the pond. Upon hatching, the tadpoles were provided with alfalfa pellets to supplement the algae present in the pools.

Experimental design

The experiment followed a $5 \times 2 \times 2$ completely randomized design, whereby tadpoles were exposed to 1 of 5 conditioning treatments (water, salamander odour, and 1, 2 or 4 conditioning of injured conspecific cues paired with salamander odour) and tested for 1 of 2 cues (water or salamander odour) at 1–2 or 11–12 days post-conditioning. Conditioning took place over a period of 2 days, with tadpoles receiving cues twice a day, once in the morning and once in the afternoon. Tadpoles were conditioned in groups in conditioning pails. Tadpoles from each conditioning pail were then tested for the two cues at the two different dates. Thus, while tadpoles were tested independently, conditioning pail was introduced as a nested factor in the analysis, to account for the non-independence of the conditioning event for those tadpoles. The average size ($\pm$SD) of tadpoles after testing (11 days post-conditioning) was 22.8 ± 1.9 mm total length.

Conditioning phase

Two weeks after hatching, 15 tadpoles (Gosner stage 25, Gosner 1960) were placed into each of 50 plastic conditioning pails (3.7 L, containing 3 L of well water) and fed alfalfa pellets. The 50 pails were randomly designated to each of the 5 conditioning treatments. After a 24-h acclimation, the conditioning phase started. All tadpoles, regardless of treatment, received a cue injection twice a day for 2 days, once in the morning (between 10:00 and 12:00 h) and once in the afternoon (between 16:00 and 18:00 h). Tadpoles were exposed to 1 of 5 treatments, summarized in Table 1: (1) water—tadpoles received 30 mL of well water, twice a day for 2 days. (2) Salamander odour—tadpoles received 20 mL of salamander odour + 10 mL of well water, twice a day for 2 days. (3) 1 conditioning—tadpoles received 30 mL of well water twice on day 1, and received 30 mL of water in the morning of day 2 and 10 mL of injured conspecific cues + 20 mL of salamander odour in the afternoon of day 2. (4) 2 conditionings—tadpoles received 30 mL of water twice on

Table 1 Summary of treatments

Treatment	Day 1		Day 2	
	Morning	Afternoon	Morning	Afternoon
Water	W	W	W	W
Salamander odour	SO	SO	SO	SO
1 Conditioning	W	W	W	TP+SO
2 Conditionings	W	W	TP+SO	TP+SO
4 Conditionings	TP+SO	TP+SO	TP+SO	TP+SO

W water; *SO* salamander odour; *TP* injured tadpole cues

day 1, and received 10 mL of injured conspecific cues + 20 mL of salamander twice on day 2. (5) 4 conditionings—tadpoles received 10 mL of injured conspecific cues + 20 mL of salamander, twice a day for 2 days. One hour after each stimulus injection, each conditioning pail received a 100 % water change, and fresh alfalfa was provided to the tadpoles.

Injured tadpoles cues were prepared a few minutes prior to use. A single batch was prepared at each conditioning time, so as to provide the tadpoles from each conditioning pail with the same stimulus. The number of tadpoles required for the conditioning event was calculated so as to provide the equivalent of 3 injured tadpoles per conditioning pail receiving the injured tadpole cue stimulus ($\sim$1 tadpole/L). Using a well-established protocol (Chivers et al. 1999; Ferrari et al. 2009a), tadpoles were euthanized with a blow to the head, the stimulus solution homogenized using a mortar and pestle, and water added to reach the desired volume (10 mL per conditioning pail). The solution was filtered through glass wool and introduced into the pails using a 10-mL syringe.

Salamander odour was prepared 1 week prior to the start of the experiment, frozen in 500-mL aliquots and subsequently thawed prior to use in the experiment. Six adult tiger salamanders (snout vent length range, 12.5–14.2 cm), each housed individually in plastic pails filled with 1.5 L of well water, were left to soak for 24 h. After this period, salamanders were paired, and the soaking water (i.e. odour) of the 2 individuals was combined and frozen in 500-mL aliquots. This procedure was repeated for 4 consecutive days. Aliquots used for each conditioning and testing event were randomly chosen among those available. Salamanders were maintained on an earthworm diet for 2 weeks and were fed the day before the stimulus collection.

Testing phase

Testing took place 1–2 and 11–12 days after conditioning. From each conditioning pail, 6 tadpoles were tested 1–2 days post-conditioning and 6 tadpoles 11–12 days post-conditioning. From those 6 tadpoles, 3 were tested for

their response to water, while the other 3 for their response to salamander odour. Testing took place between 1000 and 1800 h. The order of testing was randomized within and between days.

Individual tadpoles were placed in 0.5-L testing cups (12 cm diameter) and left to acclimate for 1 h. The behavioural assay consisted of (1) observing the behaviour of the tadpoles for 4 min, (2) injecting the stimulus in the cup (water or salamander) and (3) observing the behaviour of the tadpoles for 4 min. The injection consisted of injecting 5 mL of water or salamander odour in the cup. The cues were injected on the side of the cup, using a 5-mL syringe, to minimize disturbance associated with cue injection. The change in behaviour between the pre- and post-injection represents the behavioural response to the cue. The behaviour we recorded was a measure of activity, as a widespread antipredator response in tadpoles is to decrease activity (Chivers and Mirza 2001; Ferrari and Chivers 2011). A line was drawn in the middle of cup, and during each of the 4-min observation period, we measured the number of times the tadpole crossed the line. A line was considered crossed when the entire body of the tadpoles had crossed the line.

Statistical analysis

Raw behavioural data (number of lines crossed during the pre- and the post-stimulus periods) were computed into a per cent change in activity from the prestimulus baseline ((post–pre)/pre). Due to the high number of factors in the design and the temporal effects of the 'testing day' treatment, we analysed the data from each testing day independently using two identical analyses. For each testing day, the effects of conditioning treatment, testing cue and conditioning pail on tadpole behaviour were analysed using a 3-way nested ANOVA. To investigate interactions between conditioning treatments and testing cues, the effects of conditioning treatments were compared within each cue. Homoscedasticity assumptions were met.

Results

One day post-conditioning

Tadpoles' behaviour was significantly affected by both conditioning treatment and testing cue (conditioning × cue: $F_{4,35.9} = 3.9$, $P = 0.01$). When looking at the responses of tadpoles to water only, we found no effect of conditioning treatment ($F_{4,36.9} = 1.2$, $P = 0.3$). However, when looking at the responses of tadpoles to salamander odour, we found treatment to have a significant effect ($F_{4,69} = 14.8$, $P < 0.001$). Tukey's HSD post hoc tests

revealed that tadpoles conditioned with water or salamander odour only did not respond to salamander odour, while tadpoles conditioned with injured tadpole cues did. In addition, they responded to the salamander odour with the same intensity, regardless of the number of conditioning they experienced (see Fig. 1a). Pail had no effect of the behavioural response of the tadpoles (all $P > 0.1$).

Eleven day post-conditioning

Similarly to day 1, tadpole behaviour was significantly affected by conditioning treatment and testing cue (conditioning × cue: $F_{4,40.2} = 6.6$, $P < 0.001$). Again, conditioning treatment did not affect the response of tadpoles to water ($F_{4,41.8} = 0.1$, $P = 0.9$). For tadpoles exposed to salamander odour, we found that pail did not affect tadpoles' behaviour ($F_{43,80} = 1.3$, $P = 0.1$), but conditioning treatment did ($F_{4,40.6} = 11.5$, $P < 0.001$). Tukey's HSD tests revealed that tadpoles conditioned with water, salamander odour only or receiving 1 conditioning with injured tadpole cues did not respond to salamander odour. Tadpoles receiving 2 or 4 conditioning events responded to salamander odour, with an increase in the intensity of antipredator response as the number of conditionings with alarm cues increased (Fig. 1b). Pail did not affect the response of the tadpoles (all $P > 0.1$).

Discussion

The results of our study demonstrate the differential effects of multiple conditionings on the learning and retention of predator-related information. First, our results indicate that increasing the number of conditioning events does not increase the risk level associated with the learned response to the predator. Tadpoles conditioned 1, 2 or 4 times with injured tadpole cues paired with salamander odour did not differ in their responses to salamander odour. These results concur with previous literature on learning via injured cues. Ferrari et al. (2005) found that, given the naivety of the prey to predator odour, the concentration of injured conspecific cues was the only factor used by prey to attribute a level of risk to the newly learned predator. Fathead minnows (*Pimephales promelas*) conditioned with low concentrations of injured conspecific cues paired with predator odour subsequently recognized the predator as a low threat, while minnows conditioned with high concentrations of cues recognized the predator as a high threat. The same pattern is seen in woodfrog tadpoles (Ferrari et al. 2009a). From a learning standpoint, increasing the number of conditioning events did not seem to impact the responses of tadpoles to the predator. This contrasts with a study by Vilhunen (2006), who showed that Arctic charr (*Salvelinus*
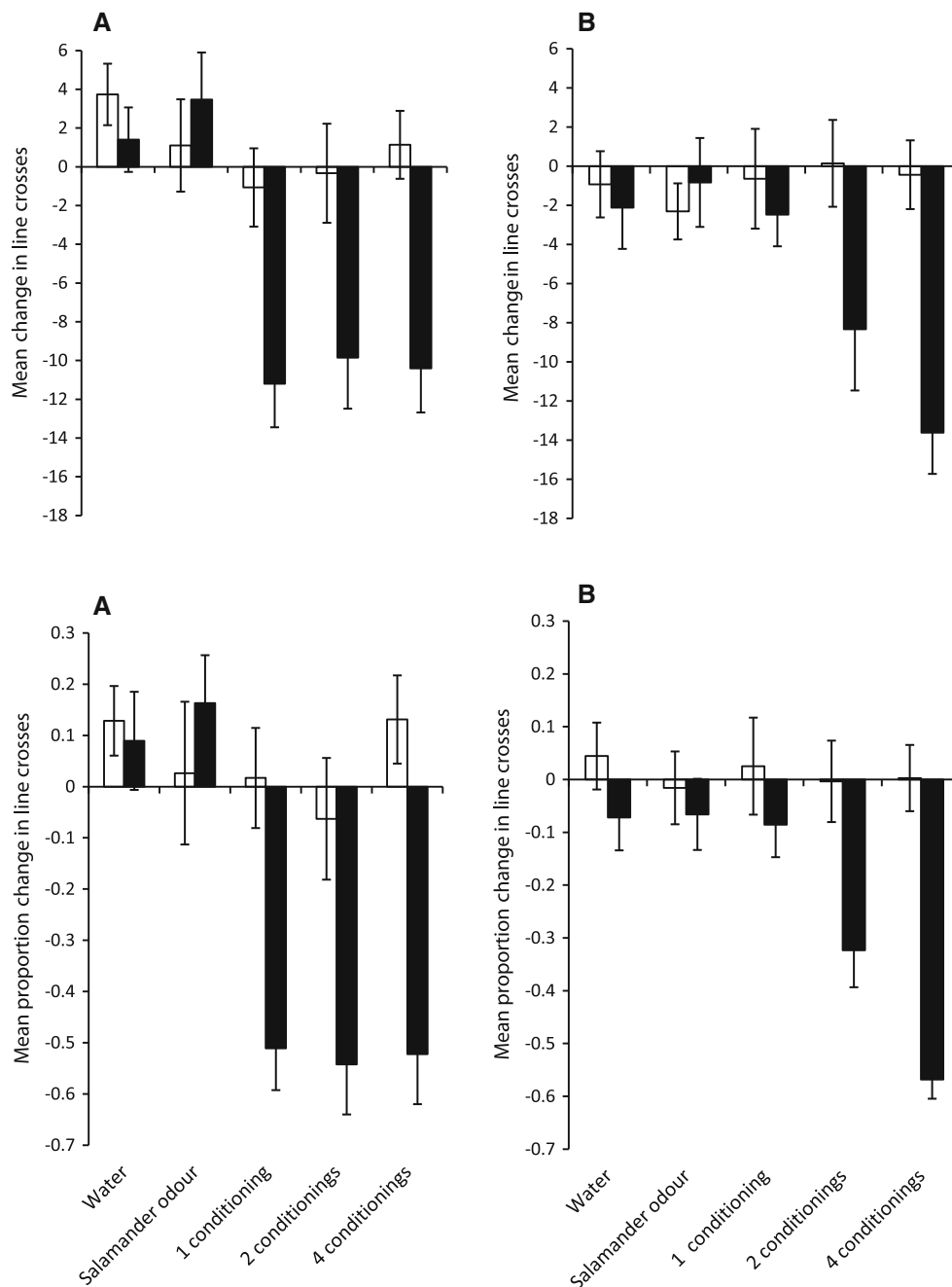
Fig. 1 Mean (±SE) change in line crosses (*top panel*) and proportion change in line crosses (*bottom panel*) from the prestimulus baseline for tadpoles exposed to water (*empty bars*) or salamander odour (*solid bars*) 1 day post-conditioning (**a**) or 11 days post-conditioning (**b**).

Tadpoles were conditioned with injured tadpole cues paired with salamander odour 1, 2 or 4 times, or received water only or salamander odour only (see text for details)

alpinus) conditioned 4 times to recognize a predatory pikeperch (*Sander lucioperca*) had higher survival than those conditioned only once. However, Vilhunen (2006) did not look at their results from a memory standpoint. In our study, an increase in the number of conditionings did not influence the intensity of the response to the predator, but instead affected the retention of the information. Given that Vilhunen tested the survival of their trout at least

4 days after the last bout of conditioning, it is possible that the fish having experienced one conditioning had a lower response to the predator than those conditioned 4 times. Studies of salmonids have shown that young-of-the-year can stop responding to a predator as early as 8 days post-conditioning (Ferrari et al. 2010b; Brown et al. 2011).

When looking at the change in the responses of tadpoles to salamander after 10 days, our results indicate that

tadpoles conditioned with fewer events respond to the salamander with a weaker antipredator response than those conditioned many times. These results indicate that the retention was affected, not by the initial risk level associated with the predator, but rather the number of times the information was presented to the individual. Keeping a behavioural ecology framework, this can be interpreted as a dimension of certainty, whereby repetition provides additional support or evidence for the labelling of the newly learned species as a predator. Can multiple conditioning events represent something other than certainty associated with the predatory status of the salamander? In other words, can something else, besides the number of conditionings per se, explain the longer memory? One possibility is that the longer memory is a reflection of the threat level posed by the predator. Previous studies with both tadpoles and fishes have shown that when prey animals learn the identity of a predator as a high threat, through conditioning with a higher concentration of injured conspecific cues, then the retention of information related to those predators is longer (Ferrari et al. 2010a, b). In our study, we did not manipulate the concentration of alarm cues. Although some may argue that repeated conditionings may increase the level of threat of the predator, we think that if the risk of the predator per se was altered, then the differential response would be seen as early as day 1. Our results show that the intensity of the learned response to the salamander was not different between the 1, 2 and 4 conditioning groups. Consequently, we argue that certainty, and not perceived risk, is the factor that determines differential response intensities in our experiment.

There are a handful of studies that have reported the duration for which prey individuals maintain a response to learned predators (Chivers and Smith 1994; Mirza and Chivers 2000; Gonzalo et al. 2009). However, only a couple have attempted to explain why different individuals or species would differ in the duration of retention of predator-related information (Ferrari et al. 2010a, 2011; Brown et al. 2011). The model of adaptive predator recognition memory developed by Ferrari et al. (2010a) identified a number of factors that should, in theory, influence the memory window of prey animals. It is clear that retaining responses to predators that prey have outgrown, for instance, is costly to the prey. They would be wasting time and energy responding to species that no longer pose a threat. With this idea in mind, Brown et al. (2011) tested whether the rate of growth of individual juvenile trout, independent of the size of the trout, has an influence on retention of predator-related information. They found that fish on a high growth rate trajectory at the time of learning maintained an overt antipredator response to the predator for a shorter duration than those on a low growth rate trajectory. Similar results were found in

woodfrog tadpoles (Ferrari et al. 2011). In addition to risk intensity and growth rate, our study provides support for an additional factor, namely certainty, which needs to be considered when investigating retention of information in prey animals.

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