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Linking predator risk and uncertainty to adaptive forgetting: a theoretical framework and empirical test using tadpoles

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Hundreds of studies have examined how prey animals assess their risk of predation. These studies work from the basic tenet that prey need to continually balance the conflicting demands of predator avoidance with activities such as foraging and reproduction. The information that animals gain regarding local predation risk is most often learned. Yet, the concept of ‘memory’ in the context of predation remains virtually unexplored. Here, our goal was (i) to determine if the memory window associated with predator recognition is fixed or flexible and, if it is flexible, (ii) to identify which factors affect the length of this window and in which ways. We performed an experiment on larval wood frogs, *Rana sylvatica*, to test whether the risk posed by, and the uncertainty associated with, the predator would affect the length of the tadpoles’ memory window. We found that as the risk associated with the predator increases, tadpoles retained predator-related information for longer. Moreover, if the uncertainty about predator-related information increases, then prey use this information for a shorter period. We also present a theoretical framework aiming at highlighting both intrinsic and extrinsic factors that could affect the memory window of information use by prey individuals.

Keywords: antipredator behaviour; predator recognition; learning; adaptive forgetting; decision-making; information use; wood frog *Rana sylvatica*

1. INTRODUCTION

Individuals seldom have complete knowledge about their environment and thus have to rely on some cues as a proxy of the quality (i.e. costs and benefits) associated with a given habitat, food patch, etc. (hereafter referred to as the environment). As time passes, the association between the cue an individual uses to assess the quality of the environment and the actual quality of the environment may become less reliable, until it reaches a point where the informative value of the cue is not different from random. When cue devaluation reaches a given threshold, one could thus predict that the individual would perform better if it did not rely on this cue to infer the best behavioural option to pursue, and an adaptive way to do this would be to ‘forget’ the cue.

The dual concept of learning and memory (Bouton 1994; Shettleworth 1998) has primarily been examined in the context of foraging and patch use and has led to the development of a few theoretical models predicting optimal information use and differential weighting processes of present versus past information by individuals. In some models, the retention of the acquired information was kept fixed (e.g. McNamara & Houston 1987). In such cases, it was predicted that in constant environments, an individual would perform best if it averaged all information using the arithmetic mean (all events contribute equally to the decision; Killeen 1981). However, if

the environment is variable, recent (and accurate) information should contribute more to the decision than older information; hence, exponential weighting of information recentness should lead to optimal decisions (e.g. McNamara & Houston 1987; Devenport & Devenport 1994; Hirvonen *et al.* 1999). Additional models have kept this variance-related exponential weighting of information but have introduced the concept of memory devaluation, for which a flexible temporal cut-off allows memories to persist for longer or shorter times according to the pay-offs they provide (e.g. Hirvonen *et al.* 1999).

By contrast with the number of models looking at optimal memory in a foraging context, to our knowledge, no model has looked at optimal memory in the context of predation. When prey collect information about their predators, how long should they rely on it before it becomes obsolete? Should we expect such a model to be different from those proposed for foraging? In foraging contexts, the uncertainty linked to patch profitability is largely due to extrinsic factors, such as whether the patch has been replenished, or whether competitors have already visited the patch recently, none of which is influenced by the individual *per se*. Using suboptimal information results in time and energy wasted, potentially leading to lower fitness. In a predation context, the variation affecting the value of information can be extrinsic, that is, unrelated to the individual. Predator community composition may change through time, and predators, if still present, may switch their diets. Maintaining both useless and inaccurate information about predators is costly (Dukas 1999; Mery & Kawecki 2005). However, unlike

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classical memory foraging models, an individual's state can also affect the value of the information, as predation risk is likely to vary with an individual's intrinsic characteristics. In this context, we define 'state' as a condition that will affect the vulnerability of the prey in the medium or long term; we are not discussing shorter term states, such as hunger level, that vary from moment to moment. The threat posed by a predator will change as a prey individual grows, changes its escape probability (e.g. runs or swims slower or faster) and exhibits behavioural, physiological and/or morphological defences that will alter its chances of being attacked. Moreover, given the unforgiving nature of predation, the cost of using suboptimal information will be much more costly for a prey than for a predator (forager).

Despite the lack of attention, both theoretical and empirical, paid to adaptive predator memory, a few studies have nevertheless investigated the memory retrieval window of some prey species. Chivers & Smith (1994) showed that fathead minnows, *Pimephales promelas*, trained to recognize either northern pike, *Esox lucius*, or goldfish, *Carassius auratus*, as predators, retained the recognition of the two species for at least two months without further reinforcement, although minnows subsequently displayed a stronger intensity of antipredator response to pike (natural predator) than to goldfish. Hazlett *et al.* (2002) similarly showed that some species of crayfish retained the responses to predators for longer than others. For salmonids, it appears that the window of memory after a single learning event is between 10 days (Mirza & Chivers 2000) and 21 days (Brown & Smith 1998). Gonzalo *et al.* (2009) showed that Iberian green frog, *Pelophylax perezi*, tadpoles maintain a response to learned predators up to 9 days. Note that while optimal models discuss the concept of memory, empirical work, thus far, cannot distinguish between memory *per se* and adaptive decision-making. In all the examples presented above, the individuals stopped displaying an overt antipredator response to the predator cues. Are these observations a result of individuals having no recollection of the learning event, that is, learned information was encoded, consolidated, but could not be retrieved (Shettleworth 1998)? Alternatively, do individuals recognize the cues but decide to ignore them in their decision-making process? For the purpose of this paper, we will leave aside this proximate argument and will rather focus on the ultimate behavioural outcome. To maintain continuity between the theoretical and empirical literature, we will cast our results within the framework of 'memory retrieval window', referred to as 'memory window' hereafter.

While different prey species may possess different memory windows for various reasons, another aspect of this line of work is (i) to find out if the memory window associated with predator recognition is fixed or flexible and, if it is flexible, (ii) to identify which factors affect the length of this window. In our experiment, we first tested whether the risk level associated with the predator (whether the predator is perceived as a high risk or as a low risk) could influence the memory window of larval wood frogs, *Rana sylvatica*. Naive individuals were taught to recognize a novel tiger salamander, *Ambystoma tigrinum*, as a high or low threat through simultaneous exposure to a high or a low concentration of injured

conspecific cues paired with salamander odour. This methodology has been shown to elicit learned predator recognition in a wide variety of aquatic species (reviewed by Ferrari *et al.* in press). In addition, the use of different concentrations of injured conspecific cues results in differential intensity of learned responses to a novel predator (Ferrari *et al.* 2009). Tadpoles were then tested either 2 or 18 days post-conditioning for their responses to salamander odour. Secondly, we tested whether uncertainty associated with the identity of the predator could influence the memory window. Previous work demonstrated that prey could respond to novel species upon their first encounter, if the species was closely related to a known predator, although with a greater uncertainty (Griffin *et al.* 2001; Ferrari *et al.* 2007). Here, we used a red-bellied newt, *Cynops pyrrhogaster*, as a novel but closely related species to tiger salamanders and tested wood frog tadpoles for their recognition of red-bellied newts either 2 or 18 days after the tadpoles learn the tiger salamander as a threat. For the purpose of this study, we have used predator identity (familiarity) as an indicator of uncertainty.

2. MATERIAL AND METHODS

(a) *Water, predators and test species*

Four weeks prior to starting the experiment, an outdoor 1900 l tub was filled with well water and seeded with zooplankton, phytoplankton and aquatic plants obtained from a pond at our field site, using a fine mesh dip net. This ensured that our holding and test water did not contain any cues from salamanders. Tiger salamanders occur in the region of our field site but our previous research indicates that no salamanders inhabit our study pond and that wood frog tadpoles do not show any innate recognition of salamander cues (Ferrari *et al.* 2009).

Wood frog egg clutches were collected in early May 2009 from a pond in central Alberta. Six clutches were transferred into a plastic pool filled with pond water and left floating on the pond to equalize the temperature of the pool water with the temperature of the pond water. After hatching, the tadpoles were provided with rabbit chow to supplement the algae already present in the pool. The tadpoles were raised for two weeks before being used in our experiments.

Three tiger salamanders (snout-vent length (SVL): mean \pm s.d. = 9.1 ± 0.4 cm) were caught from a pond on the campus of the University of Saskatchewan in April 2009 using Gee's improved minnow traps. The three salamanders were kept in a plastic tub containing 30 l of well water and fed earthworms. Four red-bellied newts (SVL: 4.0 ± 0.3 mm) and two goldfish (fork length: 7.1 ± 0.5 cm) were purchased from a local pet store and were housed individually in plastic containers filled with well water. The newts were fed newt bites (HBH Newt and Salamander Bites, Pet Products, Springville, UT, USA) and goldfish were fed fish flakes (Nutrafin Max Goldfish Flake Food, Rolf C. Hagen Inc., Montreal, Canada).

(b) *Stimulus preparation*

Predator odours were prepared prior to the start of the experiment and frozen until needed. To control for differences in body size between species, we prepared odours made from one salamander, four newts and two goldfish. To avoid any problem with using the odour of a single salamander,

salamander odours were made from three salamanders independently, and the cues from each salamander were randomly used throughout the experiment. Odours were obtained from soaking the live animals (one salamander, four newts or two goldfish) in 2 l of well water for 24 h. After this period, the stimulus was frozen in 200 ml aliquots at -20°C . The procedure was repeated for four consecutive days. The stimuli were thawed and brought to ambient temperature for use.

(c) Experimental design

The experiment consisted of conditioning tadpoles to recognize the odour of salamander as a high, low or no threat and testing them for a response to salamander odour, newt odour or goldfish odour after 2 and 18 days. The tadpoles were conditioned independently and half of them were tested at each of the two dates, so that each tadpole was only tested once in the experiment.

(i) Conditioning

Individual tadpoles were placed in 0.5 l plastic cups filled with well water and left undisturbed for 40 min. Following this acclimation period, tadpoles were exposed to 5 ml of a high or low concentration of crushed tadpole cues or water paired with 5 ml of salamander odour. The crushed tadpole cues were obtained by crushing 96 (high concentration) or 12 (low concentration) tadpoles with a mortar and pestle and adding 480 ml of well water (Ferrari *et al.* 2009). The solution was filtered through glass wool to remove any tissue. The solution was made fresh, a few minutes prior to being used. No observations were carried out during this procedure. One hour following the conditioning period, tadpoles having received the same treatment were placed in a container filled with well water and given food. They were left undisturbed until testing. Approximately 200 tadpoles were conditioned over a 2-day period. Tadpoles conditioned on different days were housed in separate containers.

(ii) Testing schedule and behavioural assay

Testing took place 2 or 18 days following the conditioning. One hour before testing, individual tadpoles were placed in 0.5 l cups filled with well water. Tadpoles were exposed to 5 ml of salamander odour, newt odour or goldfish odour. We used a well-established behavioural protocol to quantify the antipredator responses of tadpoles (e.g. Ferrari *et al.* 2009). The typical antipredator response of larval amphibians, including wood frog tadpoles, is to decrease their activity upon the detection of predation cues. Thus, a line was drawn on the bottom of the testing cups and the number of times a line was crossed was recorded during the pre- and post-stimulus periods. We considered a line was crossed when the entire body of the tadpole was on the other side of the line. The order of testing was randomized. Each tadpole was only tested once, at day 2 or day 18. We tested a total of 359 tadpoles ($n = 19 - 25/\text{treatment}$). The observer was blind with respect to the treatments.

(d) Statistical analysis

We calculated the change in proportion of line crosses from the pre-stimulus baseline. The data were normally distributed but the variances were not homogeneous among treatments. Thus, we used a non-parametric ANOVA approach (Scheirer–Ray–Hare extension of the Kruskal–Wallis test; Sokal & Rohlf 2003), whereby the effects of ‘conditioning cues’ (water versus low or high alarm cues), ‘testing

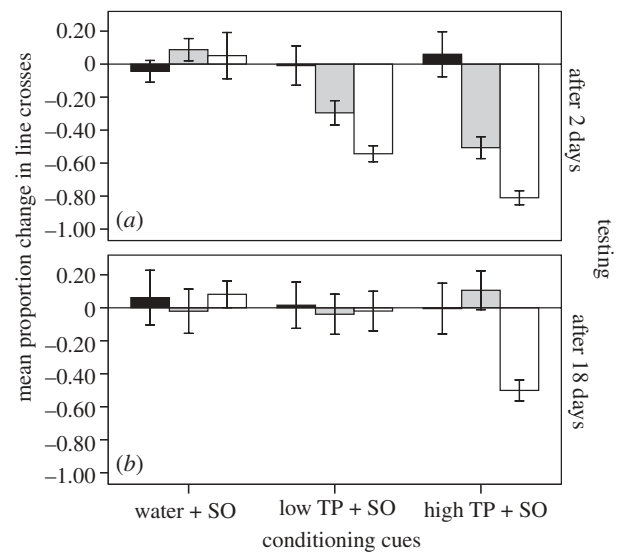


Figure 1. Mean (\pm s.e.) proportion change in line crosses from the pre-stimulus baseline for tadpoles exposed to fish odour (black bars), newt odour (grey bars) or salamander odour (white bars). Tadpoles were conditioned with salamander odour paired with water (water + SO), a low (low TP + SO) or a high (high TP + SO) concentration of crushed tadpole cues and were subsequently tested for their responses either (a) 2 days or (b) 18 days after conditioning.

cues’ (salamander, newt or fish odour) and ‘time’ (day 2 or 18) were treated as fixed factors. The simple main effects and two-way interactions were assessed post hoc.

3. RESULTS

The three-way interaction of our non-parametric ANOVA indicated that time elapsed (time), predator risk level (conditioning cues) and predator identity (test cues) all influenced the behavioural responses of tadpoles ($p < 0.01$). More specifically, we observed a two-way interaction between time elapsed and predator identity ($F_{2,353} = 5.2$, $p = 0.006$) and between time elapsed and predator risk ($F_{2,353} = 3.8$, $p = 0.023$).

(a) Tadpoles conditioned with water + salamander odour

The behavioural responses of tadpoles were similar, regardless of time elapsed ($H_{1,110} = 0.4$, $p > 0.5$; figure 1) or predator identity ($H_{2,110} = 0.6$, $p > 0.5$). There was no significant interaction between the two factors ($H_{2,110} = 1.0$, $p > 0.3$). Tadpoles conditioned with water paired with salamander odour did not respond differently to the odour of the three species.

(b) Tadpoles conditioned with a low concentration of alarm cues + salamander odour

A significant interaction was found between time elapsed and predator identity ($H_{2,114} = 4.0$, $p < 0.02$; figure 1) on the responses of tadpoles. On day 2, tadpoles responded with a different intensity to the three odours ($H_{2,65} = 10.2$, $p < 0.001$), displaying their strongest response to the salamander, a weaker one to newt and not responding to fish. On day 18, however, tadpoles did not respond to any of these cues ($H_{2,49} = 0.02$, $p > 0.9$).

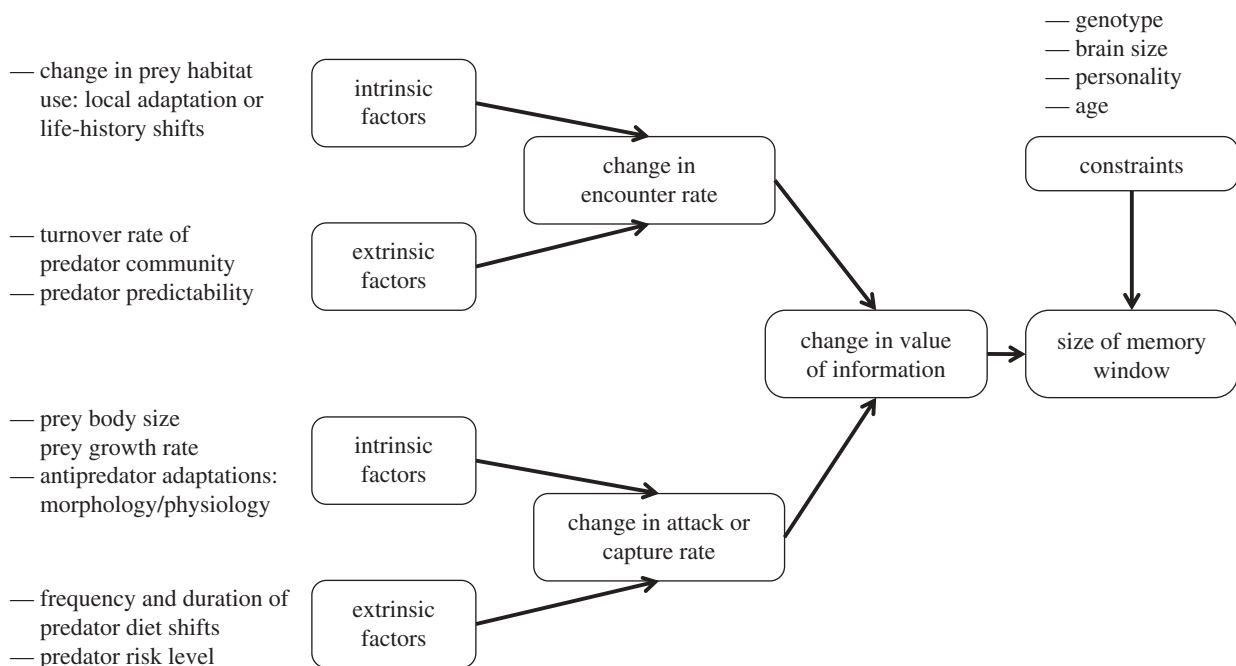


Figure 2. List of factors that may affect the size of the memory window in prey individuals. The initial memory window will depend on species-specific but also individual-specific constraints. As time passes, the value of the information related to the predator will change owing to both prey-mediated (intrinsic) and predator-mediated (extrinsic) factors that will affect the encounter rate between prey and predator, and the rate of predator attack and/or capture.

(c) Tadpoles conditioned with a high concentration of alarm cues + salamander odour

As for the tadpoles from the low alarm cue concentration group, an interaction was found between time elapsed and predator identity ($H_{2,117} = 9.0$, $p < 0.001$; figure 1). On day 2, tadpoles responded with different intensity to the odours ($H_{2,69} = 37.5$, $p < 0.001$), displaying their strongest response to the salamander odour, a weaker one to newt odour and not responding to fish odour. The responses were stronger than the ones observed from the low concentration groups. On day 18, tadpoles responded differentially to the cues ($H_{2,48} = 10.1$, $p < 0.001$), responding to salamander odour with an antipredator response, but not responding to newt or fish odour.

4. DISCUSSION

Our results indicate that the memory window of tadpoles is influenced by both the risk posed by and the uncertainty associated with predators. Tadpoles that learned to recognize the salamander as a high threat responded to salamander cues after 18 days, whereas tadpoles that learned to recognize the salamander as a low threat did not. In addition, when the uncertainty associated with the identity (familiarity) of the predator was higher, the rate of forgetting was also greater. Tadpoles that learned to recognize salamanders as predators responded to closely related newts but did not respond to goldfish. Moreover, the intensity of antipredator response displayed to the newt was lower than that displayed to the salamander (figure 1a). These results support previous findings (Ferrari *et al.* 2007, 2009). The lower response intensity displayed to the closely related species does not reflect the risk level associated with the novel species (i.e. that the newt is in fact less risky than the salamander), but rather reflects uncertainty, that is, the

perceived probability of the novel species indeed being a predator given that a closely related species is a predator. When tested 2 days post-conditioning, tadpoles responded to both salamander and newt odours. When tested 18 days post-conditioning, tadpoles still responded to the salamander, although with a lower response intensity, but did not respond to the newt. One could argue that the absence of the response is due to the additive effect of the reduction in intensity through time paired with the lower intensity displayed to the newt odour; however, the response pattern is not a simple result of additive lower responses. On day 2, tadpoles from the low concentration of alarm cue group responded to the salamander odour with an approximately 50 per cent reduction in activity level, but still responded to the newt with an approximately 30 per cent reduction in activity level. On day 18, tadpoles from the group exposed to a high concentration of alarm cue responded to the salamander odour with an approximately 50 per cent reduction in the activity level, but did not decrease their activity upon detecting the newt odour (parametric ANOVA: time: $F_{1,78} = 44$, $p < 0.001$; predator (salamander versus newt): $F_{1,78} = 43$, $p < 0.001$; interaction: $F_{1,78} = 5$, $p = 0.032$). This observation indicates that the response associated with the newt is not simply an extrapolation of the responses associated with the salamander. In the context of memory, the devaluation rate related to information about the newt is different from that of the salamander and is likely due to the differential uncertainty (familiarity) associated with the two predators.

While previous studies have reported different memory windows for different species of prey, our study is the first to identify parameters that affect this window. We have identified a number of other factors, both intrinsic and extrinsic, that may influence the size of the memory window of prey species (figure 2). First, we start with a

'default' memory window that is set by some morphological and genetic parameters. The plasticity of the memory window will be linked to the individual's evolutionary history (see below).

(a) Extrinsic factors affecting memory windows of prey

Extrinsic factors that should affect the length of the memory window include turnover rate of the predator community and the frequency of diet shifts displayed by the predators. If predators are not present in the environment any more or not foraging on the prey, then maintaining obsolete information about the risk associated with that predator will lead to an overestimation of risk and the use of suboptimal risk-averse behaviours. Factors reinforcing the knowledge of the presence and the risk of the predators, such as encounter rate, probability of attack and success rate, will elicit the proper memory windows for that predator. If the predator is predictable, cues used to predict predator presence will be of high informative value and should thus be remembered for longer.

(b) Intrinsic factors affecting memory windows

A number of intrinsic factors can act to decrease a prey's memory window. As the prey grows, it may be exposed to a new community of predators, either by outgrowing their previous predators, or by ontogenetic shifts in habitats (Werner *et al.* 1983). In addition, prey may develop or increase behavioural, morphological and physiological adaptations that will decrease their risk of being successfully attacked or may deter predators altogether (Chivers *et al.* 2008); hence, while undergoing these ontogenetic changes, prey may have a shorter memory. Conversely, prey individuals that reach their adult size and maintain their vulnerability status should have a longer memory window. As we showed here, information reliability also affects the memory window of prey. Unreliable information could result from information collected socially, through unreliable or inexperienced individuals (e.g. Hare & Atkins 2001), or could result from the prey having incomplete information about the identity or risk of a predator. As the reliability and accuracy of the information increases, the memory window should be longer. Age is an interesting factor to take into account when considering the memory window. The memory window of a young individual is limited by its age (Dunlap *et al.* 2009), that is, a young individual cannot have a memory window greater than the time it has been alive. As the individual gets older, selection should favour an optimal memory window size, as pre-reproductive adults will suffer the greatest costs in terms of reproductive loss owing to suboptimal decisions. However, as prey approach senescence, and their reproductive potential decreases (assuming those individuals are not semelparous), the costs of using suboptimal information will be lowered. Thus, the difference between the predicted optimal and the observed memory windows of prey individuals may be negatively correlated with fitness potential. Factors listed in figure 2 are not exhaustive, but should provide a good starting point for studies on the adaptiveness of forgetting in the context of predation. Studies able to tease apart risk and uncertainty might

reveal interesting patterns in term of information retention that we could not uncover with our design. In addition, studies looking at the plasticity of memory windows across contexts (predation, foraging and habitat choice) should be fruitful.

As uncertainty about the informative value of environmental cues increases, individuals should perform better by ignoring these cues in their decision-making. It appears that the existence of a memory window serves that purpose. However, the rate of cue devaluation will be linked to the rate of environmental change: in a slow-changing environment, the cue should stay informative for longer than in a fast-changing environment (McNamara & Houston 1987). The 'default' memory window that different species have should be dependent on their evolutionary history. On an evolutionary time scale, populations or species occurring in slow-changing environments should have a longer 'default' memory window than those evolving in fast-changing environments. However, species that evolved with the greatest variability in environmental changes (i.e. from slow to fast) should have the greatest plasticity in their memory windows. This aspect of species evolutionary history may be crucial in predicting and explaining the existence of ecological traps. Ecological traps occur when individuals are misled into choosing a suboptimal habitat through the use of environmental cues that used to, but no longer reflect the real quality of the habitat type (Robertson & Hutto 2006). Nowadays, such discrepancy between habitat quality and habitat cues is often the result of anthropogenic activities (e.g. Kriska *et al.* 1998; Weldon & Haddad 2005). More empirical work focusing on adaptive forgetting is needed to provide ecologists with a better understanding of factors that affect the ability of individuals to make optimal decisions.

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