

# Learning, memorizing and apparent forgetting of chemical cues from new predators by Iberian green frog tadpoles

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**Abstract** Many antipredator adaptations are induced by the prey's ability to recognize chemical cues from predators. However, predator recognition often requires learning by prey individuals. Iberian green frog tadpoles (*Pelophylax perezi*) have the ability to learn new potential predators. Here, we tested the memory capabilities of Iberian green frog tadpoles. We conditioned tadpoles with chemicals cues from a non-predatory fish in conjunction with conspecific alarm cues, and examined whether tadpoles retained their conditioned response (reduction of activity level). We found that conditioned tadpoles reduced their activity levels in subsequent exposures to the non-predatory fish cues alone. Tadpoles were able to remember this association and reduced movement rate at least for 9 days after. The ability to learn and memorize potential predators may be especially important for the survivorship of prey species that are likely to find a high variety of predators. However, after those 9 days, there was a lack of response to the non-predatory fish cues alone in the absence of reinforcement. This could be explained if tadpoles behave according to the threat-sensitive predator avoidance hypothesis, and the perceived risk to the learning cue diminished over time, or it could be due to an apparent forgetting process to avoid non-adaptative responses to chemical cues of non-dangerous species that were randomly paired with alarm cues. Thus, this study demonstrates that green frog tadpoles in the absence of reinforcement remember the chemical cues of a learned

predator only for a limited time that may be adaptive in a threat-sensitive context.

**Keywords** Alarm cues · Memory · Predation risk · Predator recognition · Frogs · *Pelophylax perezi*

## Introduction

Predators often induce shifts in prey behavior and anti-predatory behavior is often mediated by the prey's ability to recognize chemical cues from predators and to react according to the threat level posed by that predator (Lima and Dill 1990; Lima 1998). Failure to respond to a potential predator may be fatal. However, unnecessary anti-predatory behavior may have direct energetic costs as well as costs associated with reduced opportunity to feed or reproduce (Lima and Dill 1990). Sensory information obtained about a predator may assist an organism in assessing the potential risk accurately and, therefore, reduce these costs (Lima and Dill 1990; Chivers and Smith 1998). Experience with predation cues is an important element in the development of antipredator behavior in a wide range of vertebrates (Von Frisch 1938; Petranka et al. 1987; Kiesecker et al. 1996; Chivers and Smith 1998) as well as invertebrates (Dodson et al. 1994; Jacobsen and Stabell 2004; see review in Kats and Dill 1998). Therefore, learning may conceivably affect several aspects of anti-predator behavior and experience may enhance the ability to recognize predators.

In aquatic environments, reception of chemical cues released by predators and injured prey is an important sensory mode by which most prey gather information about the threat of predation (Dodson et al. 1994; Chivers and Smith 1998; Kats and Dill 1998). There are a variety of

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chemical cues associated with predation, some from the predator (kairomones) and other cues released by injured prey (i.e., alarm cues; Chivers and Smith 1998; Kats and Dill 1998). Chemical alarm cues are important in facilitating learned recognition of predation risk by prey animals such as many fishes (Göz 1941; Magurran 1989; Mathis and Smith 1993; Chivers and Smith 1994a, 1998; Larson and McCormick 2005), adult newts (Woody and Mathis 1998) or frog and toad tadpoles (Mirza et al 2006; Gonzalo et al. 2007). Releaser induced recognition learning involves the simultaneous exposure to an aversive stimulus and a neutral stimulus causing learned aversion to the neutral stimuli (Yunker et al. 1999). The result of this learning mechanism is acquired predator recognition in which predator naïve individuals show appropriate anti-predator behavior to the cue of a potential predator even though they have had no direct exposure to the predator. Several authors have showed such acquired predator recognition by pairing alarm cues with the visual or chemical cues of a predator (e.g., Chivers and Smith 1994a; Larson and McCormick 2005; Gonzalo et al. 2007).

Although numerous studies have investigated learning, less attention has been directed at memory. Learning and memory are linked; there is little point to learn if the information cannot be recalled and remembered. However, the processes are distinct, and there are differences between them. Learning is essentially the acquisition of memory, whereas memory has other composites, such as retention and the potential for interference (Shettleworth 1998). European and fathead minnows, after learning predator recognition by conditioning them with alarm cues, retain the memory of the potential predator and respond to their signals a few days to several weeks after (Magurran 1989; Chivers and Smith 1994a, b; Brown and Smith 1998; Mirza and Chivers 2000). Also, different species of crayfish present different times of retention of the learning response (Hazlett et al. 2002). Research directed at quantifying memory duration, how rates of forgetting progress or what factors cause variation in forgetting rates is far less common than studies investigating the acquisition of information (Shettleworth 1998). Some studies in the past have interpreted failure to continue to respond to certain stimuli as memory “failure” with potentially negative fitness consequences. However, since adaptive forgetting was proposed (Kraemer and Golding 1997), very few studies have explored this topic (Brown et al 2002; Golub and Brown 2003; Hawkins et al. 2007).

Amphibians can learn that unknown cues are dangerous when these unknown cues are mixed with conspecific alarm cues (Mirza et al. 2006; Gonzalo et al. 2007). Even cues from non-predatory species can be learned as dangerous (Gonzalo et al. 2007). However, the potential retention of this learning association in amphibians remains

unexplored. The aim of this study was to examine the retention in the near future of a conditioned response to a “new” predator by Iberian green frog tadpoles (*Pelophylax perezi*, formerly *Rana perezi*), and discuss the possible adaptive significance of the lack of this response in a threat-sensitive context.

Iberian green frogs live and breed in different kinds of aquatic habitats (García-París 2000) with a wide range of types of predators. Also, tadpoles of these frogs have long periods of growth before metamorphosis (García-París 2000), and their predator species vary across seasons. A previous study showed that Iberian green frog tadpoles that had been exposed to non-predatory fish chemical cues mixed with conspecific alarm cues responded 2 days later to the “new” predator (non-predatory fish) cues alone with a reduction of activity (Gonzalo et al. 2007). Thus, learning and memory could be especially important mechanisms for the survivorship of tadpoles and for accurately assessing the risk posed by a predator. Then, to test the duration of the response to a “new” predator in the near future, we conditioned Iberian green frog tadpoles with chemicals cues from a non-predatory fish (i.e., cues not previously associated with danger) in conjunction with conspecific alarm cues, and examined whether tadpoles retained their conditioned response.

## Materials and methods

### Study animals

We collected 185 Iberian green frog tadpoles (Body length,  $\bar{X} + SE = 5.4 \pm 0.2$  cm; Gosner’s stage = 25; see Gosner 1960) by netting during July of 2007 at several small ponds in Collado Mediano (Madrid, Central Spain). Tadpoles were housed in groups of five tadpoles at “El Ventorrillo” Field Station, 10 km from the capture area, in plastic aquaria (49 × 29 cm and 25 cm high) with 5 L of water at ambient temperature and under a natural photoperiod. They were fed every day with commercial fish flakes.

We obtained from a commercial dealer non-predatory zebra danio fish (*Brachydanio rerio*) to be used as source of neutral scent. Before and after the end of the experiment, fishes were maintained in a large filtered aquarium and regularly fed with commercial fish flakes.

All the animals were healthy during the trials; all maintained or increased their original body mass.

### Preparation of chemical stimuli

Alarm cues of tadpoles were prepared from three tadpoles (body length,  $\bar{X} \pm SE = 4.2 \pm 0.1$  cm). They were cold

anesthetized by placing at 4°C for 20 min, inducing deep hypothermia, and, then were euthanized with a quick blow to the head to avoid suffering (ASIH 2004). We did not use a chemical anesthetic because these chemicals may interfere with natural tadpoles' chemical cues in subsequent trials. The extract was prepared by putting these dead tadpoles in a clean disposable plastic dish, and macerating them in 3,000 mL of distilled water. The stimulus water was filtered through absorbent paper to remove solid particles, and immediately frozen in 10 mL portions until used (Woody and Mathis 1998).

The fish stimulus was prepared by placing ten zebra danio fishes into a 10 L aquarium with clean water for 3 days. These aquaria were aerated but not filtered. Fishes were not fed during this short period to avoid contaminating water with food odor. Thereafter, water was drawn from the aquaria and frozen in 10 mL portions until its use in experiments. Fishes were returned and fed in their home aquaria. We prepared control water in an identical manner, but without placing fish in the aquaria (Woody and Mathis 1998).

#### Experimental design

We randomly assigned each group of five tadpoles to two different treatments (control group,  $N = 90$ ; or experimental group,  $N = 90$ ). On the first day of the experiment tadpoles from the 'control' treatment were exposed to the fish chemical cues alone mixed with clean water. At the same time, tadpoles from the 'experimental' treatment were exposed to both the scent of the fish and conspecific chemical alarm cues, thus, simulating the cues from a predatory fish that was eating a conspecific tadpole. A previous study showed that tadpoles conditioned with these mix of stimuli (fish and alarm cues) were 2 days later able to recognize the fish chemical cues alone as coming from a predator (Gonzalo et al. 2007). Thus, experimental tadpoles were considered as conditioned. The conditioning events (control and experimental) were carried on in the tadpoles' home plastic aquaria (49 × 29 cm and 25 cm high) to avoid stress due to transfer from one aquaria to another. We made different conditioning solutions, 20 mL each (2 ice aliquots), using combinations of clean water with fish chemical cues, and alarm cues with fish chemical cues. After ice aliquots were thawed we pipetted conditioning solutions in the center of the aquaria.

To test for the duration of the response to this predator recognition, on days 3, 6, 9, 12, 15, or 18 after the initial conditioning, different individuals from the two treatments were tested with the fish chemical cues alone in clean water. Fifteen individuals from the two groups were tested at the same time in parallel and observations were carried out blind to the tadpole treatment. Each day, we tested 15

individuals from each of the two groups (control and experimental). These tadpoles were chosen randomly from the several groups we had. After the trial, tadpoles were kept separately and not used in subsequent trials. New individual tadpoles were used in each trial to ensure that we were just testing the capacity of retention of the learning association. We could not use the same individual tadpoles in more than one test because successive exposures without reinforcement could lead to learning the innocuousness of the "non-dangerous" predator (Hazlett 2003) or habituation to the predator cues, so that the results of the experiment would not reflect duration of the response alone.

Tadpoles were tested individually in gray, U-shaped gutters (101 × 11 cm and 6 cm high) sealed at both ends with plastic caps (see Rohr and Madison 2001 for detailed descriptions). We marked the internal part of the gutters with four crossing lines that created five subdivisions of equal surface. We filled each gutter with 3 L of clean water (20°C) from a mountain spring, which did not contain fish. We placed clear plastic over each trough on either side of the cage to isolate the system from air movements in the testing room (see Rohr and Madison 2001). Each trial lasted for 1 h and consisted of a 30 min pre-stimulus period and a 30 min post-stimulus period separated by a stimulus introduction. We assigned test solutions (10 mL of fish scent) to one end of each trough (right or left) by stratified randomization, and assigned 10 mL of clean water to the opposite end. We placed a single tadpole in each gutter, and waited 5 min for acclimation. Then, we started the 'pre-stimulus' test (30 min). Thereafter, we added the test solution and, then, immediately started the 'post-stimulus' period (30 min). During the pre- and the post-stimulus periods, we recorded from a blind quadrant that each tadpole occupied at 1-min interval for 30 min. We calculated the number of lines crossed for all periods and this was considered as an index of general activity (Rohr and Madison 2001; Gonzalo et al. 2007). Diffusion of chemicals in still water may be a slow process. However, all individual tadpoles used in the experiment were observed at least once in all of the subdivisions of the gutter, so we were confident that all tadpoles were really exposed to the chemical stimuli. Moreover, tadpoles often showed episodes of fast swimming that should contribute to diffuse chemicals in water.

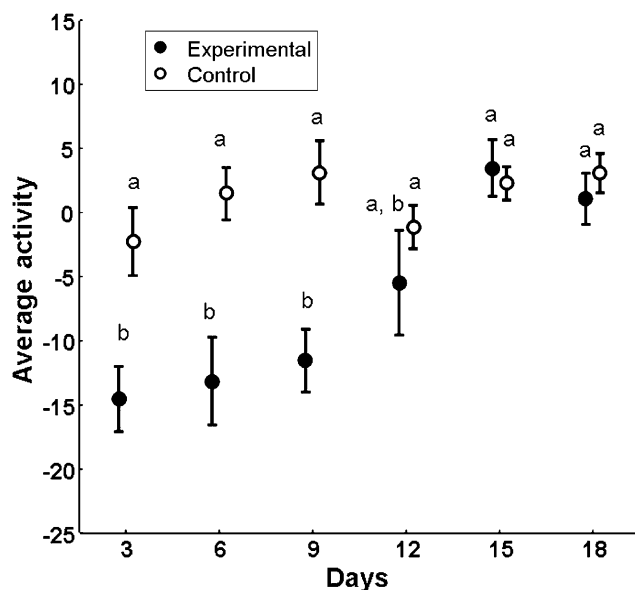
#### Data analyses

For each trial, we calculated levels of activity as the difference between the numbers of line crossed between the pre- and post-stimulus periods. Positive values indicate increased movement following the addition of stimulus; negative values indicate decreased activity. Data were log-transformed to ensure normality (Shapiro–Wilk's tests,

$P > 0.05$  in all cases) and homogeneity of variances (Levene's tests,  $P > 0.05$  in all cases), and then tested by general linear modeling (GLM; Grafen and Hails 2002). We used 'day' of the trial (i.e., number of days since the initial conditioning event) and 'conditioning' (i.e., control treatment conditioning with the absence of alarm cues vs. experimental treatment conditioning with the presence of alarm cues) as categorical variables. We included the interactions between variables in the model to test for the effects of the different treatments (conditioned with or without alarm cues) depending on the day of the trial. Subsequent post hoc multiple comparisons were made using Tukey's pairwise comparisons (Sokal and Rohlf 1995).

## Results

On an average, control tadpoles were more active than experimental tadpoles conditioned with conspecific alarm cue ('conditioning' effect  $F_{1,168} = 31.05$ ,  $P < 0.0001$ ; Fig. 1). Also, there were significant differences between the different days of the trials ('days' effect  $F_{5,168} = 6.45$ ,  $P = 0.0016$ ). Therefore, the overall activity of tadpoles increased over time since the initial conditioning event. However, the interaction between factors was significant ( $F_{5,168} = 3.76$ ,  $P = 0.002$ ; Fig. 1). Thus, 3 days after the initial conditioning event experimental tadpoles, previously exposed to a combination of alarm cues and fish odor; significantly decreased activity in comparison with control



**Fig. 1** Mean ( $\pm$ SE) activity level (i.e., difference between the numbers of line crossing between the pre and post-stimulus periods) of experimental and control tadpoles when exposed to non-predatory fish alone, at several days after initial conditioning with fish cues mixed with conspecific alarm cues. Different letters above bars indicate significant differences (Tukey's tests,  $P < 0.05$ )

tadpoles (Tukey's test  $P = 0.02$ ), the same difference was noted six ( $P = 0.001$ ) and 9 days ( $P = 0.003$ ) after the conditioning event. However, on days 12, 15, and 18, there were no significant differences in the activity between experimental and control tadpoles ( $P \geq 0.90$  in all cases). Although, there were no significant differences in activity level between days for the control tadpoles ( $P \geq 0.05$  in all cases), there were significant differences between the experimental tadpoles depending on the day; activity of experimental tadpoles did not differ on days 3, 6, and 9 ( $P \geq 0.90$  in all cases), but activity was significantly lower on these days than on days 15 and 18 ( $P < 0.02$  in all cases), which were not significantly different between them ( $P = 0.90$ ). Beginning on day 12 and each test day thereafter, activity of experimental tadpoles was not significantly different from the activity of experimental tadpoles ( $P \geq 0.20$  in all cases).

## Discussion

Our results showed that 3, 6 and 9 days after exposure to chemical cues from the potential predatory fish, the experimental Iberian green frog tadpoles displayed anti-predator behaviors (i.e., a reduction in activity) in response to these chemical cues, suggesting that tadpoles still remembered the learned cue association 9 days after exposure. After 12 days, the initial conditioning, mean activity of experimental tadpoles in response to fish chemical cues was higher but variance was also high, suggesting that some of the experimental tadpoles, but not others, still were able to react to the fish as a predator. In contrast, at 15 and 18 days postexposure, experimental tadpoles did not show any anti-predator behavior, and behaved as the control tadpoles. Several studies showed that fishes are able to retain the memory of the potential predator and respond to their signals a few days to several months after (Chivers and Smith 1998; Brown and Smith 1998, Berejikian et al. 1999; Mirza and Chivers 2000). These studies also reported that the response became weak over time, which suggests that reinforcement may be necessary to maintain the intensity of the response. Hawkins et al. (2007) showed that, in fishes, the learned responses disappear as the prey individual gets larger and outgrow the predator. However, in our experiment, tadpoles did not increase significantly their size across the experiment, and zebra danio fish used as scent donors were smaller than tadpoles from the beginning of the experiment. This suggests that tadpoles could not accurately assess the size of the fish and it rejects that the lack of antipredator response might be due to tadpoles' growth. Thus, our data showed a decline in response that can also be attributed to the lack of reinforcement.

The ability to learn and memorize the potential predators may be especially important for the survivorship of prey species that are likely to find a high variety of predators while they are in the aquatic phase. Thus, learning and memory may enable animals to adjust their behavior in variable environments. However, to always respond to a chemical cue as dangerous only because it coincidentally appeared once mixed with chemical alarm cues could be very costly (Lima and Dill 1990). In those circumstances, longer the time interval between successive contacts with a particular cue labeled as “dangerous”, the more likely that it was not actually dangerous. Thus, the lack of antipredator response, far from a failed memory, could be a powerful strategy for dealing with conflicting information. In another experiment (Gonzalo et al. 2007) Iberian green frog tadpoles behaved according to the threat-sensitive predator avoidance hypothesis (Helfman 1989) when they were confronted with a native predator snake (to which they innately react, Gonzalo et al. unpublished data). Thus, snakes were not perceived to be very dangerous predators unless the tadpoles had been previously exposed to snakes that ‘had eaten conspecifics’ (i.e., mix of alarm cues plus snake chemical cues). According to the threat-sensitive predator avoidance hypothesis, prey species should behave flexibly towards a varying degree of predator threat and, consequently, leave more time for other activities when the threat is low (Helfman 1989). If tadpoles reacted weakly to a natural and familiar predator that is not actually attacking tadpoles, it is possible that they were assessing risk based on the predator diet and adaptively balancing the costs and benefits of predator avoidance. In the present study, we gave tadpoles incomplete or unreliable information regarding a new predator identity, allowing them only to “smell” a new potential predator. Because tadpoles did not have other additional information on the actual risk of this particular predator, the selection of an anti-predator behavior should be informed by recent experiences (Turner et al. 2005; Ferrari and Chivers 2006). Thus, as time goes on from the encounter with the potential predator, the perceived risk would diminish over time from the exposure to the conditioning event and fish perceived as low-risk predators due to the lack of reinforcement. It would also allow tadpoles to show avoidance behaviors only in the face of active predators and high-predation risk, and to reduce costs associated with unnecessary anti-predatory behavior. This hypothesis is supported by a range of studies examining memory that have revealed that, even after apparent forgetting, a latent (residual) memory persists and can be revealed by facilitated acquisition in a subsequent learning event (Plotkin and Oakley 1975; Matzel et al. 1992; Monk et al. 1996; Nicholson et al. 2003; Philips et al. 2006). Thus, a memory may outlast its behavioral expression.

However, Philips et al. (2006) also found that in water snails, latent memory to attacks with electric shocks decayed at 4 days. Thus, the lack of antipredator response could also be due to a real forgetting phenomenon (Philips et al. 2006). Traditionally, forgetting was considered a failing of memory, but over the past decades researchers have moved towards the idea that the ability to forget may be advantageous (Kraemer and Golding 1997). Learning and memory allow animals to adjust their behavior to adapt to changeable environments and thus cope with a degree of unpredictability (Shettleworth 1998). In such environments, animals that use learning and memory to hone their behavior will have advantages over other more behaviorally fixed individuals. However, animals continually receive information about their environment and must filter this information to focus on those aspects most important to survival (Dukas 2002). Thus, prey are often confronted with multiple types of potential predators, and a response caused by a coincidental pairing of unrelated cues inducing antipredator behavior could prove very costly to prey species. Forgetting processes that help map an animal’s behavior to the instabilities inherent in a changing environment could, thus, contribute to survival (Hendersen 1985). In natural conditions, tadpoles have to encounter a wide range of mixed cues (e.g., alarm cues, predator cues, non-predator cues). As we see in the present study, to elicit an antipredator response to predator cues during the first days, even overestimating the potential risk level, could be adaptive because tadpoles had recent passed through a conditioning event of biological importance (learning a new dangerous predator). However, as time passes and tadpoles do not face up the same ‘predator that had eaten conspecifics’ (i.e., the mix of fish cues with alarm cue), the possibility of the two cues accidentally appearing together increases. Therefore, to lose the tendency to respond to the previous association could be adaptive, because it may prevent tadpoles to do not persevere with maladaptive antipredator behaviors towards non-dangerous species that live in the same habitat.

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