

# Threat-sensitive generalization of predator recognition by larval amphibians

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**Abstract** Despite the importance of acquired predator recognition in mediating predator–prey interactions, we know little about the specific characteristics that prey use to distinguish predators from non-predators. Recent experiments with mammals and fish indicate that some prey lacking innate predator recognition have the ability to display anti-predator responses upon their first encounter with those predators if they are similar to predators that the prey has recently learned to recognize. This phenomenon is referred to as generalization of predator recognition. In this experiment, we documented for the first time that larval amphibians (woodfrog, *Rana sylvatica*) have the ability to generalize the recognition of known predators to closely related novel predators. Moreover, we demonstrated that this ability is dependent on the level of risk associated with the known predator. When red-bellied newt, *Cynops pyrrhogaster* (known predator), was paired with simulated low risk, tadpoles displayed fright responses to newts and novel tiger salamanders, *Ambystoma tigrinum*, but not to novel African clawed frogs, *Xenopus laevis*. However, when the newt was paired with simulated high risk, tadpoles generalized their responses to both tiger salamanders and African clawed frogs. Larval anurans seem to have a wider generalization frame than other animals.

**Keywords** Generalization · Predator recognition · Threat sensitivity · Predator odor · Larval amphibians · Woodfrog *Rana sylvatica*

## Introduction

Prey have to constantly balance predator avoidance and other fitness-related activities such as foraging and reproduction. Hence, prey individuals should adjust the intensity of their anti-predator responses to match the level of risk posed by the predator in order to optimize this trade-off (Helfman 1989; Chivers et al. 2001). An obvious prerequisite for prey to display adaptive responses to predators is being able to recognize potential predators as threats. A number of prey species have the ability to recognize their predators without any prior experience with them. This ‘innate’ predator recognition has been studied in a variety of taxa, including mammals, birds, amphibians, and fishes (e.g., Kiesecker and Blaustein 1997; Berejikian et al. 2003; Fendt 2006). For other species lacking this ability, learning is therefore a necessary step.

Learned predator recognition can occur through a variety of mechanisms, including direct encounters with predators or through social learning (mammals—Griffin and Evans 2003, birds—Vieth et al. 1980, fishes—Mathis et al. 1996). For aquatic prey, a widespread mode of learning is through the pairing of injured conspecific cues with the odor or sight of a novel predator (e.g., larval amphibians—Woody and Mathis 1998, Mirza et al. 2006; fishes—Mathis and Smith 1993; aquatic invertebrates—Wisenden and Millard 2001, Hazlett 2003). This represents a classical conditioned learning paradigm, in which the predator odor acts as a conditioned stimulus (previously unknown stimulus) and the alarm cues act as an unconditioned stimulus (stimulus

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that inherently elicits a fright response). After being simultaneously exposed to the conditioned and unconditioned stimulus, prey learn to exhibit a fright response to the predator odor alone. During a single learning event, prey not only learn to recognize the odor or sight of a novel predator (e.g., Chivers and Smith 1994a, b) but also the risk associated with this predator (e.g., Ferrari et al. 2005, 2006). When prey are exposed to high concentrations of alarm cues paired with predator odor, they recognize the predator as a high risk, but when they are exposed to the predator with low concentrations of alarm cues, they recognize it as a low risk (Dupuch et al. 2004; Ferrari et al. 2005, 2006, 2008b; Kesavaraju et al. 2007).

While much research has shown that prey can learn to recognize predators from non-predators, we know surprisingly little about the specific characteristics that prey use to recognize a predator as threatening. Moreover, we know little about whether prey can generalize their anti-predator responses to other predators that are similar to ones the prey has learned to recognize. Early studies indicated that squirrel monkeys did not generalize their fear responses from a model cat to a model snake (Herzog and Hopf 1984) and rhesus monkeys did not generalize their fear responses from a snake to an electric cord or a wood block (Mineka and Cook 1988). These results lie in stark contrast to four studies demonstrating generalization of predator recognition. In each of these cases, the predator cues used were much more realistic than the ones used by Mineka and Cook (1988) and Herzog and Hopf (1984). Griffin et al. (2001) demonstrated that predator-naïve tammar wallabies (*Macropus eugenii*) presented with a model red fox (*Vulpes vulpes*), a model cat (*Felis catus*), or a model goat (*Capra hircus*) do not display any anti-predator responses. However, when wallabies were conditioned to recognize a model red fox as a predator, the wallabies not only displayed a fearful response to the red fox model but also to the feral cat model. Hence, wallabies labeled feral cats as threatening based on the morphological similarities between the fox and the cat. Stankowich and Coss (2007) exposed wild black-tailed deer (*Odocoileus hemionus columbianus*) to models of a mule deer (control), a jaguar, a tiger, and a cougar, with cougars being the only predator occurring in this region. They found that deer displayed fearful responses to the cougar model, as expected, but also to the jaguar models, indicating that deer generalized their recognition to another felid predator based on the morphological similarities between the species. However, it is unknown if deer have an innate or a learned anti-predator response to cougars. While these studies investigated the generalization of predator recognition based on visual cues, Ferrari et al. (2007a) provided evidence that the same phenomenon occurred for prey using chemosensory cues to recognize predators. Fathead minnows (*Pimephales prom-*

*elas*) were conditioned to recognize the odor of lake trout (*Salvelinus namaycush*) as threatening, and subsequently tested for their response to the odor of lake trout (reference predator), brook trout (*Salvelinus fontinalis*, same order as lake trout), rainbow trout (*Oncorhynchus mykiss*, same family as lake trout), Northern pike (*Esox lucius*, predator from a different order), and white sucker (*Catostomus commersoni*, non-predator from a different order). They found that minnows did not subsequently recognize the pike or the sucker but did recognize the three species of trout as dangerous. Interestingly, the intensity of their anti-predator responses was inversely proportional to the relatedness of the species to the reference predator (i.e., the minnows responded more to the brook trout than the rainbow trout). In a follow-up experiment, Ferrari et al. (2008a) demonstrated that generalization in minnows was not constant but rather depended on the risk associated with the reference predator. Minnows generalized to closely related predators when the reference predator was recognized as a high-risk predator, but not when the predator was recognized as a low-risk predator.

While the concept of generalization of predator recognition has received limited interest from a behavioral ecology perspective, stimulus generalization has received the most attention from psychologists. Stimulus generalization has been reported using different sensory modalities (sounds and light), in a variety of taxa (from insects to mammals), in several biological contexts (foraging and courtship) and seems independent of experience with the stimulus (reviewed by Guirlanda and Enquist 2003). A response can be evoked upon exposure to a particular stimulus (e.g., a sound or a light of a given frequency) but also to stimuli that are ‘similar’ to that stimulus (sound or light of a slightly different frequency). The intensity of the response to the test stimulus decreases as the frequency deviates from the learned frequency. Put back in the context of predator recognition, the ability of prey to respond to a variety of stimuli that are ‘similar’ to the ones the prey already recognize as dangerous can have important survival consequences.

In this study, we investigated (1) the ability of larval amphibians to generalize their recognition of predators, (2) the extent to which they do so, and (3) whether their generalization is constant or dependant on the level of risk associated with the reference predator. Woodfrog tadpoles do not have innate recognition of salamander predators (e.g., Ferrari et al. 2007b) and, hence, have to learn to recognize them. We conditioned larval woodfrogs to recognize red-bellied newts (*Cynops pyrrhogaster*, allopatric species) as a predator by exposing them to newt odor paired with different concentrations of injured conspecific cues. Tadpoles conditioned with higher concentrations of injured cues should learn to recognize the newt as a higher

risk than tadpoles conditioned with lower concentrations of injured cues. We then tested the tadpoles for their response to the odor of newts (reference predator), tiger salamanders (*Ambystoma tigrinum*—different family than the newt), or African clawed frogs (*Xenopus laevis*—different order).

## Methods

### Water, test subjects, and predators

Two weeks prior to starting the experiments, a 1,900-L water trough was filled with water pumped from an underground well and left outdoors. The water was seeded with zooplankton and phytoplankton from a local pond using a fine mesh dip net. This ensured that the holding and testing water contained a full array of algae and plankton but no amphibian cues that could possibly be present in any local pond water. This water is referred to as ‘well water’ hereafter.

Six woodfrog egg clutches were collected in early May from a local pond, and transferred into a pool (60 cm diameter) containing pond water and aquatic plants. The pool was positioned on the pond to equalize the temperature of the pool water with the pond water. After hatching, the tadpoles were raised for 2 weeks. Rabbit food was provided to supplement the algae already present in the pool.

Six red-bellied newts (snout-vent length (svl)—mean $\pm$ S.D.=6.4 $\pm$ 0.8 cm), one tiger salamander (svl=14.1 cm), and two African clawed frogs (svl=6.1 and 9.1 cm) were obtained from a commercial supplier and maintained by the Biology Department Animal Care Unit from the University of Saskatchewan. Different numbers of animals were chosen to approximate the same volume of predator to produce the cues, using a volume-displacement method. Newts and frogs were fed floating food sticks (ReptoMin, Tetrafauna—Tetra Holding (US) Inc., Blacksburg, VA, USA), while the salamander was maintained on a live cricket and earthworm diet.

### Experimental procedure

The experiment consisted of a conditioning phase followed by a testing phase. During the conditioning phase, the tadpoles were exposed to newt odor paired with either a high, medium, or low concentration of injured conspecific cues or a water control to generate groups of tadpoles with differential learning of the risk associated with the newt (Ferrari et al. 2005). To ensure that the concentrations of injured cues used would produce groups of tadpoles having statistically different intensities of anti-predator response, a subgroup of tadpoles from each of the four groups were

observed during this phase and their anti-predator intensity was recorded and compared. Because the responses of tadpoles from the medium and high concentration groups did not statistically differ, the medium concentration group was removed from the experiment for the testing phase. During the testing phase, the tadpoles from the remaining groups (water, low and high concentration groups) were exposed to the odor of newt, salamander, or frog and the intensity of their anti-predator responses was compared. The experiment was performed outdoors, under natural light regime and temperature.

### Conditioning phase: exposure to injured cues and newt odor

Two hours prior to the beginning of the experiment, individual tadpoles were placed in plastic cups (0.5 L—10 cm diameter, 12 cm high) filled with well water and left to acclimate. The conditioning procedure consisted of injecting in each cup 10 mL of a solution of newt odor followed by 5 mL of a high, medium, or low concentration solution of conspecific injured cues or 5 mL of well water. The solution of newt odor was obtained by soaking six newts in 2 L of well water for 24 h. The solutions of injured cues were obtained by crushing one tadpole in either 5 mL of well water (high concentration), 20 mL of well water (medium concentration), or 40 mL of well water (low concentration). The crushing was done using a mortar and pestle. The injured cue solutions were then filtered through glass wool to remove any remaining tissues. Both stimuli (newt odor and injured cues/water) were gently injected on the side of the cup using 10-mL syringes to minimize disturbance to the tadpoles. We conditioned 60 tadpoles in each of the four groups. Three hours after the conditioning phase, a 100% water change was performed on all cups and rabbit chow was provided to the tadpoles.

Behavioral observations were carried out on 30 randomly chosen tadpoles from each of the four conditioning groups. Larval anuran amphibians, including woodfrog tadpoles, have been shown to decrease activity in response to predation cues (Chivers and Mirza 2001; Ferrari et al. 2007b, c). Hence, a line was drawn in the middle of the cups and the number of line crosses (on the horizontal plane) was counted during the observation periods. We considered that a tadpole crossed a line when its entire body was on the other side of the line.

The trials consisted of a 4-min pre-stimulus period followed by a 4-min post-stimulus period during which the behavior of the tadpole was recorded (number of line crosses). The two periods were separated by a 45-s injection period, during which the contents of the two stimulus syringes were emptied slowly on the side of the cup to minimize disturbance. The tadpole had to cross a

minimum of six lines during the pre-stimulus period for the trial to continue (as per Ferrari et al. 2007b, c, 2008b). All the trials were performed outdoors and the order of the treatments was randomized.

Testing phase: exposure to newt, salamander, and frog odor

The medium- and high-injured cue treatment groups did not show statistically different intensities of response during the conditioning phase, hence the medium concentration group was removed from the experiment. Three days after the conditioning phase, a 100% water change was performed on all cups and the tadpoles were left to acclimate for 2 h. Each conditioning group was randomly split into three groups of 20, each group receiving 10 mL of a solution of either newt odor, salamander odor, or frog odor. The three solutions were obtained by independently soaking six newts, one salamander, and two frogs in 2 L of water for 24 h. All the tadpoles were observed during this phase. The observation procedure is identical to the one described for the conditioning phase. We tested 15–19 tadpoles in each of the nine treatments (water, low or high conditioning groups, each exposed to newt, salamander, or frog odor).

#### Statistical analysis

Statistical comparisons were performed on the percent change in line crosses from the pre-stimulus baseline ( $[\text{number of line crosses in the post-stimulus period} - \text{number of line crosses in the pre-stimulus period}] \times 100 / \text{number of line crosses in the pre-stimulus period}$ ). The data followed parametric assumptions for both the conditioning phase (Levene's test— $F_{3,115}=1.8$ ,  $P=0.15$ ) and the testing phase ( $F_{8,137}=1.3$ ,  $P=0.23$ ). To compare the effect of injured cue concentration (water, low, medium, or high concentrations) during the conditioning phase, we performed a one-way ANOVA followed by post hoc Tukey tests.

The results of the testing phase were analyzed using two-way ANOVA to assess the effect of conditioning treatment (water, low or high injured cue concentration treatments) and the effect of predator species (newt, salamander, or frog odor) on the response of the tadpoles. Due to a significant interaction between the two factors, we performed three subsequent one-way ANOVAs to investigate if tadpoles responded differently to the predators for each conditioning cue.

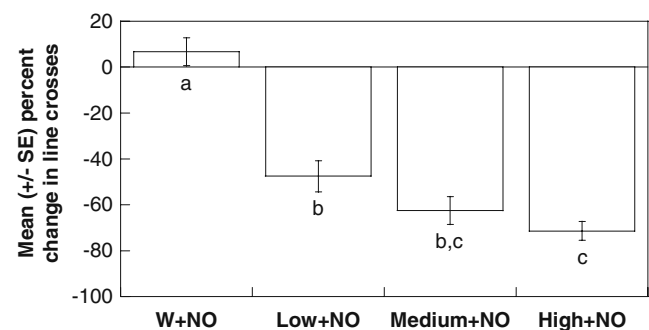
Threat-sensitive generalization could result from an additive or synergistic effect of combining threat-sensitive learning with generalization. In the case of an additive effect, there is some point where the combined effect of reduced risk and reduced specificity would fall below the threshold for evoking a significant anti-predator response.

In the case of a synergistic effect, the difference in intensity of response between the high injured cue conditioning group and low injured cue conditioning group exposed to the newt should be smaller than the difference in intensity between the high alarm and low injured cue conditioning groups in response to salamander or *Xenopus* (i.e., the response to the low-risk closely related predator should be lower than expected in the additive scenario). Consequently, to test for a possible interaction between the intensity of threat associated with the known reference predator and the response to the closely related predator, we performed a partial two-way ANOVA, comparing only two levels of threat (high and low) and the three predators. All tests were performed using SPSS 17.

## Results

### Conditioning phase

The results of the ANOVA indicated a significant effect of injured cue concentration on the responses of tadpoles ( $F_{3,115}=35.8$ ,  $P<0.001$ , Fig. 1). Post hoc comparisons revealed that tadpoles exposed to water paired with newt odor responded with a lower intensity of response than the other groups (all  $P<0.001$ ). Tadpoles exposed to the low concentration of injured cues paired with newt odor did not respond statistically differently than the tadpoles exposed to the medium concentration paired with newt odor ( $P=0.27$ , but see trend on Fig. 1), but did respond with a lower intensity than tadpoles exposed to newt odor paired with the high concentration of injured cues ( $P=0.025$ ). Tadpoles exposed to newt odor paired with the medium concentration and the high concentration of injured cues did not differ in their intensity of anti-predator response ( $P=0.70$ ).



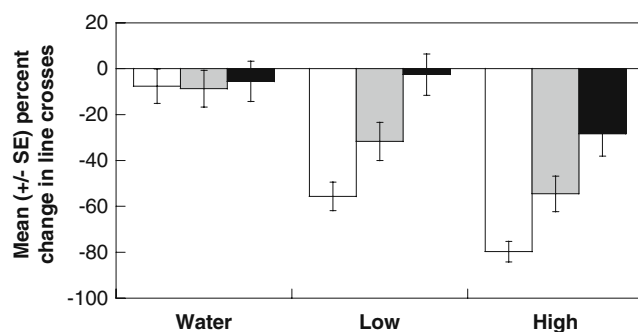
**Fig. 1** Mean ( $\pm$ S.E.) percent change in line crosses from the pre-stimulus baseline for tadpoles exposed to the odor of red-bellied newt paired with well water (*W+NO*), a low (*Low+NO*), medium (*Medium+NO*), or high (*High+NO*) concentration of injured tadpole cues. Different letters denote significant differences between treatments

## Testing phase

The 3×3 ANOVA detected a significant interaction between predator species and conditioning treatment ( $F_{4,137}=3.3$ ,  $P=0.014$ , Fig. 2). Tadpoles conditioned with water paired with newt odor did not differ in their response intensity when subsequently exposed to either newt, salamander, or frog odor ( $F_{2,43}=0.9$ ,  $P=0.38$ ). When the tadpoles were conditioned with a low or a high concentration of injured cues, however, a significant effect of predator species was found (low concentration— $F_{2,42}=12.2$ ,  $P<0.001$ ; high concentration— $F_{2,48}=11.4$ ,  $P<0.001$ ). In both cases, tadpoles responded with the strongest intensity to the newt odor, with the lowest intensity to the frog odor and with an intermediate intensity to the salamander odor. The 2×3 ANOVA revealed that the generalization phenomenon appears to result from an additive effect between reduced risk and reduced specificity from the predator (predator— $F_{2,94}=23.6$ ,  $P<0.001$ ; cue— $F_{1,94}=14.2$ ,  $P<0.001$ ; predator×cue— $F_{2,94}=0.018$ ,  $P>0.9$ ).

## Discussion

The results of our experiment indicate that, during conditioning trials, tadpoles exposed to red-bellied newts paired with increasing concentrations of injured conspecific cues respond with increasing intensities of anti-predator behavior. Moreover, the tadpoles learn to subsequently respond to the newt odor with increasing anti-predator responses (threat-sensitive learning, Ferrari et al. 2005, 2008b). Indeed, during both the conditioning and the testing phase, tadpoles conditioned with the high concentration of injured cues responded with a statistically stronger intensity than tadpoles conditioned with a low concentration of injured cues, which in turn responded with



**Fig. 2** Mean ( $\pm$ S.E.) percent change in line crosses from the pre-stimulus baseline for tadpoles conditioned with newt odor paired with water ( $W+NO$ ), a low ( $Low+NO$ ) or a high ( $High+NO$ ) concentration of injured tadpoles cues and subsequently exposed to the odor of red-bellied newt (white bars), tiger salamander (gray bars), or African clawed frog (black bars)

a statistically stronger intensity than tadpoles from the control group. These results demonstrate threat-sensitive responses to varying concentrations of injured cues and also threat-sensitive learning of predator recognition in larval amphibians. These results support previous results by Mirza et al. (2006), whose data were suggestive of threat-sensitive learning of predators by larval American toads (*Bufo americanus*). Threat-sensitive learning has already been demonstrated in other taxa (both vertebrate and invertebrate taxa), hence these results are not surprising. Nevertheless, this was a necessary step to establish in order for us to test whether generalization was dependent on the risk associated with the reference predator.

The results of the testing phase are the first to demonstrate that larval amphibians possess the ability to generalize their recognition of a known predator to closely related species of that predator. The effect we examined in this study is equivalent to increasing the intensity of the unconditioned stimulus and examining how this manipulation influences the generalization gradient. Learning theory predicts that increasing the intensity of the unconditioned stimulus will broaden the generalization (Rescorla and Wagner 1972). Our results are consistent with these predictions. Our results also support those of psychology studies undertaking conditioning experiments with arbitrary stimuli, whereby lower responses to the test stimuli occur as the test stimuli become progressively more and more different from the conditioned stimulus (Guirlanda and Enquist 2003). Generalization is not a static phenomenon but rather depends on the level of threat associated with the predator. When the newt was considered a high-threat predator (high concentration group), tadpoles displayed anti-predator responses to newt, salamander, and frog odors. However, when the newt was considered a low-risk predator, tadpoles failed to display a fright response when exposed to frog odor, and responded with a lower intensity to salamander odor.

When tadpoles were conditioned with water (control group), tadpoles did not show any innate recognition of newt, salamander, or *Xenopus* cues. This finding is consistent with our previous results from this exact pond, demonstrating that woodfrog tadpoles do not have innate recognition of tiger salamander cues (Ferrari et al. 2007b, 2008b; Ferrari and Chivers 2008), the only salamander species naturally found in our study area. When tadpoles were conditioned through pairing of newt odor and high concentrations of injured conspecific cues, they showed a significant anti-predator response not only to newt odor (the reference predator) but also to salamander and frog odors. The response to the frog is quite surprising given that it is distantly related to the other two species. In their experiments, Ferrari et al. (2007a) showed that fathead minnows could generalize their recognition of lake trout or brown

trout to other trout species but not to distantly related predators like pike or perch. The differences in the ability to generalize seen in these two studies could be explained by three hypotheses: (1) the level of risk associated with the reference predator might have been perceived as higher by the tadpoles in the current experiment than by the fish in the past experiments, (2) fish species used in previous experiments may be more distinct from each other than amphibian species used in this experiment, or (3) tadpoles may have a much wider frame of generalization than fishes, as their generalization extends to predators much more distinct. Although we cannot rule out the first two scenarios, we argue that the third is important because larval amphibian populations are exposed to greater variation in predator communities than fishes. Depending on the laying location, woodfrog tadpoles, and to a greater extent other species of amphibians with a lower breeding site fidelity, might find themselves in ephemeral ponds with no predators or at the other extreme, in wetlands with a large variety of predatory species. Fish, on the other hand, generally do not move from pond to pond, or lake to lake, and the predator community may be more constant through generations. Hence, it might be more beneficial for larval amphibians to possess a wider generalization frame to compensate for the great variability in predation pressure that they potentially experience. These results are consistent with theory on the evolution of learning (e.g., Stephens 1991) including the Predator Recognition Continuum Hypothesis proposed by Ferrari et al. (2007a). Accordingly, predator recognition is dependent on (but not limited to) the temporal and spatial predictability of predation and the diversity of the predators and non-predators in the environment. Innate predator recognition should be selected in environments where the predictability of attack from a predator is high and the diversity of predators is low (i.e., a few but constant predators). In contrast, prey exposed to a great variety of predator species that are unpredictable in their probability of attack should benefit more from learned predator recognition. This would allow a case-by-case learning of potential threats. Prey exposed to the greatest variability of predation contexts (as is the case for woodfrogs) should display the greatest plasticity in their responses to predators, of which generalization of predator recognition is included.

Prey that possess innate recognition of their predators have commonly been considered far more ‘adapted’, because they do not need a “learning trial” to recognize their predators and hence have a better survival upon their first encounter with the predator. Our results indicate that generalization may provide prey with an advantage similar to innate recognition. Indeed, tadpoles do not need to learn to recognize salamanders or clawed frogs per se to learn to be wary of them. Empirical studies of generalization of

predator recognition are at their infancy. If generalization is a widespread phenomenon among prey species, then the benefits associated with innate versus learned predator recognition might not differ as much as previously thought.

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