

Prior Experience Alters the Behavioral Response of Prey to a Nonnative Predator

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ABSTRACT.—Anuran larvae (tadpoles) can alter their behavior and morphology in response to predators with which they have coevolved. Furthermore, tadpoles of a few species are capable of learning, which can elicit or reinforce predator-avoidance behaviors. However, it remains unclear how widespread this capacity for learning is among anurans and whether it is biased in favor of evolutionarily familiar predators. Here, we test whether prior experiences will modify the behavioral response of Lowland Leopard Frog *Lithobates (Rana) yavapaiensis* tadpoles to Green Sunfish *Lepomis cyanellus*, a recently introduced predator. We exposed focal tadpoles for 10 days to the chemical and visual cues of one of three conditioning treatments: a cricket-fed Green Sunfish, a tadpole-fed Green Sunfish, or a control tank without predator. Subsequently, we measured the swimming activity of focal tadpoles in response to a neutral cue (water) and the chemical cues of Green Sunfish. No difference between conditioning treatments was observed in response to the water cue. In contrast, tadpoles that had previously experienced either of the sunfish conditioning treatments displayed significantly higher swimming activity than control tadpoles for 2–4 min after exposure to the sunfish chemical cues. Our results indicate that the behavior of tadpoles can be altered by prior experiences, even in the absence of alarm cues. In addition to providing another example of learning in tadpoles, our results suggest that tadpoles may have a broad learning template that can be applied to organisms with which they have recently come into contact.

Anuran larvae (tadpoles) have evolved a number of morphological and behavioral traits to cope with unpredictable levels of predation. For example, in the presence of predators with which they have coevolved, tadpoles can accelerate their development (Warkentin, 2000) or reduce their foraging activity (Relyea, 2001). In addition, they can develop larger tail fins and muscles, which may increase their swimming speed (although see Van Buskirk and McCollum, 2000; Van Buskirk, 2002) or deflect attacks away from the head (Van Buskirk et al., 2003, 2004). Predator-induced phenotypes presumably represent adaptive trade-offs in the presence of predation (Lima and Dill, 1990; Relyea, 2001; Van Buskirk, 2002; Álvarez and Nicieza, 2006) despite their energetic or developmental costs (Lawler, 1989; Skelly, 1992; Van Buskirk, 2000; Relyea and Auld, 2004).

The behavioral responses of prey to predators can be constitutive or phenotypically plastic. A constitutive response implies that tadpoles will display an innate predator avoidance behavior in response to evolutionarily familiar predators (Kats et al., 1988; Griffiths et al., 1998). In addition, some species of tadpoles are capable

of learning (a form of phenotypic plasticity). For example, tadpoles will display more pronounced predator-avoidance behavior after having witnessed predation events (Murray et al., 2004; Mandrillon and Saglio, 2005) or simulations thereof (Ferrari et al., 2005; Mirza et al., 2006; Gonzalo et al., 2007). The altered behavior in response to prior exposure to predators is likely to increase survival in the presence of predators (Griffin, 2004; Álvarez and Nicieza, 2006).

In aquatic taxa such as amphibians and fish, learning of predators is frequently facilitated when predators are tagged, or associated, with alarm cues—the organic compounds released from injured conspecific prey (Semlitsch and Reyer, 1992; Chivers and Smith, 1998; Kats and Dill, 1998; Summey and Mathis, 1998). For example, Mirza et al. (2006) showed that chemical alarm cues from injured conspecifics facilitate recognition of an evolutionarily familiar odonate predator in American Toad *Bufo americanus* tadpoles and that the strength of the predator-avoidance behavior correlated with the concentration of alarm cues. But learning is not universal among tadpoles (e.g., Laurila et al., 1997). For most anuran species, it is not known whether tadpoles can learn and, in instances where they do, whether they rely on alarm cues, predator-specific cues, or a combi-

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nation of both to assess predation risk (Álvarez and Nicieza, 2006).

Learning should be an effective mechanism for rapidly coping with unfamiliar situations including novel selective pressures. Consistent with this hypothesis, a few studies have demonstrated that tadpoles can learn to associate unfamiliar cues with a predation threat based on prior experiences (Marquis et al., 2004; Mandrillon and Saglio, 2005, 2007). For example, Mandrillon and Saglio (2005) showed that Common Toad *Bufo bufo* tadpoles do not innately reduce their swimming activity in the presence of the chemical cues of an inoffensive gastropod or a nonnative crayfish *Astacus leptodactylus* predator. However, tadpoles reduced their activity when presented with gastropods or crayfish cues if tadpoles had previously been exposed to gastropods or crayfish in conjunction with alarm cues (Mandrillon and Saglio, 2005). Similarly, tadpoles of the Common Frog *Rana temporaria* and the Common Toad *B. bufo* showed no predator avoidance to the cues of nonnative crayfish *A. leptodactylus*. However, tadpoles from both species significantly reduced their swimming activity if the predator had been fed tadpoles the previous day (Marquis et al., 2004). These results suggest that learning is facilitated by the presence of conspecific alarm cues in water or in a predator's waste products. Furthermore, they raise the possibility that learning, particularly by association with alarm signals, may serve as a general mechanism for coping with evolutionarily novel situations such as the sudden appearance of nonnative predators.

The objectives of this experiment were to test the following two questions: (1) Can Lowland Leopard Frog *Lithobates (Rana) yavapaiensis* tadpoles learn to recognize Green Sunfish *Lepomis cyanellus* as a predator? (2) If so, are alarm signals from consumed conspecifics necessary for learning to occur? We predicted that Lowland Leopard Frog tadpoles would associate the cues of sunfish with that of a potential threat, at least in the tadpole-fed sunfish treatment (where alarm cues are assumed to be present). Conversely, we hypothesized that tadpoles raised in the control conditioning treatment would be relatively naïve to the sunfish cue and the danger that it represented and, as a result, would not decrease their swimming activity to the same extent as the tadpoles in the two sunfish treatments.

MATERIALS AND METHODS

Study Species.—The Lowland Leopard Frog *Lithobates yavapaiensis* (formerly *Rana yavapaien-*

sis) is a rapid currently restricted in its range to the state of Arizona (Sredl, 2005). Populations of Lowland Leopard Frogs throughout the species' range have been in decline for the last several decades for a variety of reasons, including alteration of water-flow regimes, amphibian disease, and the introduction of novel predators (Rosen and Schwalbe, 2002). The Green Sunfish *L. cyanellus* is native to central regions of North America (Page and Burr, 1991) but has been introduced to Arizona, where it now preys on Lowland Leopard Frog tadpoles (Rosen and Schwalbe, 2002). The first museum records of Green Sunfish in Arizona date to 1913. By the 1960s, Green Sunfish were being collected regularly in counties throughout Arizona (Minckley SONFISH database, P. J. Unmack, Arizona State University GIS Manual for Use with the Lower Colorado Basin Fish Database, Tempe, 2002), although some regions (e.g., upper reaches of Aravaipa and Muleshoe canyons) have remained essentially free of Green Sunfish.

Population Origin and Tadpole Care.—Four partial egg clutches (approximately 100 eggs each) were collected from a sunfish-free pond in Tucson, Arizona, in April 2006 and shipped to Austin, Texas, the following day. The history of this population is not well documented, and we cannot rule out the possibility of some interactions with sunfish during previous generations. Tadpoles from different clutches were maintained separately throughout the experiment to control for clutch-specific effects. Tadpoles were reared in the lab (17–20°C, 12 : 12 D : N light regime), where they were fed a diet of 75% algae (spirulina) and 25% Tetramin flakes five times weekly.

We began our experiment when all tadpoles reached Gosner stage 25 (Gosner, 1960). We ran our experiment in 10 blocks between July and September 2006, where each block consisted of 15 full-sib tadpoles randomly assigned to one of three conditioning treatments (five tadpoles per treatment block). The conditioning period lasted 10 days and took place in 38-L aquaria, which were partitioned in half with a transparent, permeable barrier. We placed groups of five focal tadpoles on one side of the divider and the other side held one of three possible predator-conditioning treatments: empty arena (control), a cricket-fed sunfish (CFS), or a tadpole-fed sunfish (TFS). We used two different prey items (heterospecific and conspecific) to control for the release of tadpole alarm cues. In the CFS and TFS treatments, sunfish were fed five Lowland Leopard Frog tadpoles from a stock of the same population or an equivalent mass of crickets, respectively, on alternate days for 10 days. All feeder tadpoles and crickets were generally consumed within less than 1 min of feeding.

Survival of focal tadpoles during the experiment was 100%.

Experimental Design.—Learning is the process by which an organism's behavior is altered as a result of prior experience (Shettleworth, 1998). We were interested in contrasting the behavioral response of two types of tadpoles that might plausibly occur in the wild: naïve tadpoles (that are encountering a sunfish scent for the first time) and tadpoles that had previously witnessed sunfish predation events. This comparison is relevant because the manner in which tadpoles respond to sunfish cues could be influenced by prior experiences and is likely to have important fitness consequences.

Traditionally, associative learning is inferred by measuring the behavior of focal organisms in response to a conditional stimulus (e.g., novel scent) both before and after a training period, during which the conditional stimulus is associated with an unconditional stimulus (e.g., alarm cue). A change in behavior in response to the conditional stimulus as a result of the conditioning is interpreted as evidence of associative learning (Shettleworth, 1998). However, we were concerned that the stimulus (sunfish scent) being tested might not be conditional (i.e., initially not neutral) and might induce a permanently altered behavioral state. To address this concern, our methodology deviated from traditional tests of associative learning in two ways. First, we avoided using an approach in which a same individual is exposed to the cue of interest (sunfish scent) both before and after a conditioning period. Instead, we simply measured the behavioral responses of tadpoles to sunfish scent after they had been exposed to different conditioning treatments. Second, we did not alternate the order in which water and sunfish cues were tested after the conditioning period. This approach precludes us from formally testing whether tadpoles from each conditioning treatment responded differently to water and sunfish scent but ensures that naïve tadpoles have had no prior exposure to sunfish scent. We can still test whether the conditioning treatments significantly altered the behavioral responses to each cue independently and whether the difference between conditioning treatments was dependent on the nature of the presented cue because blocks controlled for the age and genetic composition of tadpoles.

Behavioral Observations.—When pursued or disturbed in the wild, free-swimming (i.e., Gosner stage 25 or above) Lowland Leopard Frogs tadpoles will exhibit a burst of rapid swimming then remain immobile under leaf-litter, silt, or vegetation on the bottom of a pond or river (MAS, pers. obs.). In the lab, Lowland

Leopard Frog tadpoles reduce their swimming activity when raised in the continuous presence of live sunfish (Sosa et al., 2009) as do tadpoles of numerous other species in response to predators (e.g., Chivers and Smith, 1998; Marquis et al., 2004; Relyea, 2004). Thus, we used a reduction in swimming activity as a measure of perceived predation risk.

The swimming activity of tadpoles within each block was quantified on three occasions: 1–2 days before the conditioning treatment ("baseline"); 1–2 days after the conditioning treatment in response to one liter of aged water (as a control for delivering the stimulus); and 1–2 days later, in response to one liter of water containing sunfish cues. The sunfish chemical cue was obtained from a tank with 25 L of aged water in which a single adult sunfish had been placed for 24 h. It is important to note that the sunfish used to make the sunfish cue had not been fed tadpoles for at least two weeks. In one study, dietary alarm cues from tadpole-fed odonate predators had no detectable effect on rapid tadpole behavior after 2–3 days (Laurila et al., 1998). Thus, we assumed that the sunfish cue would be void of any detectable alarm cue.

Swimming activity was quantified in clean 38-L tanks filled with 25 L of aged water. In all behavioral assays, tadpoles were allowed to acclimate to the tank for 5 min, and their behavior was then videotaped from behind a blind during daylight hours. For the preconditioning baseline behavior, tadpole behavior was recorded for 5 min. (The baseline behavior was recorded for only nine of the 10 blocks.) To quantify the response to each cue, tadpole behavior was recorded for 5 min, at which point a 1-L cue (either water or sunfish cue) was poured into the tank, followed by an additional 10 min of recording. In a given block, we randomized the order in which we recorded the three predator conditioning treatments.

Swimming activity was scored from video footage as the number of focal tadpoles that were "mobile" every 5 sec. Tadpoles were defined as mobile if they were either swimming or actively foraging on the tank substrate. The fraction of mobile tadpoles (out of five) in the tank was averaged over 1-min periods. Scoring was conducted by three observers who were blind to treatment. To control for interobserver effects, each block was scored by a single observer.

Statistical Analyses.—The unit of analysis was the mean percentage of five focal tadpoles swimming during a 1-min period and hereafter is termed "swimming activity." Swimming activity was analyzed using a Mixed Linear Model in SAS (Littell et al., 2006) where interbatch variation was accounted for as a random effect. Because the order of the cues (sunfish and

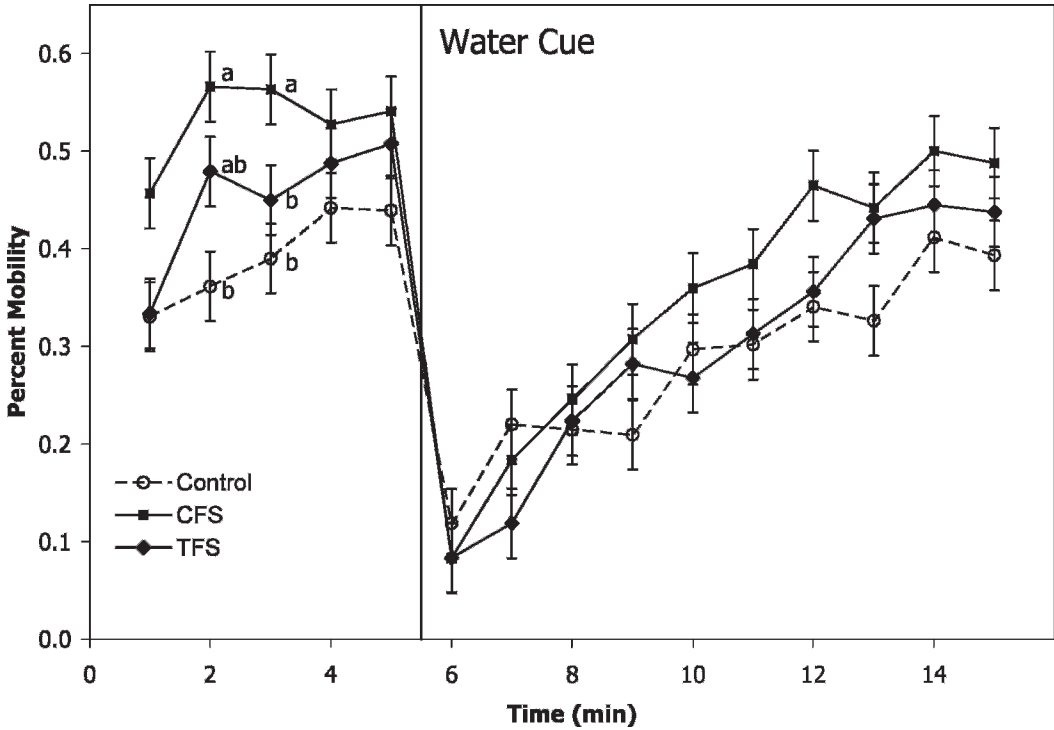


FIG. 1. Swimming activity (mean and SE percent mobile during 1-min periods) of Lowland Leopard Frog *Lithobates (Rana) yavapaiensis* tadpoles previously exposed to control, cricket-fed sunfish (CFS), or tadpole-fed sunfish (TFS) conditioning treatments for 10 days. Each point is the mean of 10 replicates, each with five tadpoles. One liter of water was applied after 5 min. Letters indicate time segments when swimming activity of tadpoles differed significantly between treatments after correction for multiple comparisons ($\alpha = 0.001$).

water) was not randomized, we did not formally test for an interaction between cue and conditioning treatment. Instead, we asked whether there were differences in swimming activity caused by conditioning treatments for each cue separately. Predator avoidance behaviors can be short lived and dissipate in minutes (e.g., Kats and Dill, 1998; Pennuto and Keppler, 2008). Therefore, our model consisted of a factorial design of MINUTE, CONDITIONING-TREATMENT, and MINUTE * CONDITIONING-TREATMENT interaction, analyzed separately for each cue. We used $\alpha = 0.05$ to evaluate the interaction. Then we used the SLICE function of the MIXED procedure to compare differences among conditioning treatments within each one-MINUTE interval. There were three comparisons (CONTROL-CFS, CONTROL-TFS, CFS-TFS) within each of the 15 MINUTES (i.e., 45 comparisons). We used a modified Bonferroni to correct for multiple comparisons: $\alpha = 0.05/45 = 0.0011$. All tests were two tailed.

RESULTS

Prior to the conditioning period, there were no differences between treatments in mean

tadpole mass ($F_{2,27} = 0.21, P = 0.814$) or baseline swimming activity ($F_{2,26} = 0.22, P = 0.671$). There were significant differences in swimming activity across time periods. All tadpoles dramatically decreased their swimming activity in response to the application of the water cue and sunfish cue (TIME [water cue] $F_{14,126} = 22.77, P < 0.0001$, Fig. 1; TIME [sunfish cue]: $F_{14,126} = 47.87, P < 0.0001$, Fig. 2). Swimming activity returned almost to baseline levels within approximately 7–10 min (Figs. 1 and 2).

The swimming activity of tadpoles did not differ between conditioning treatments after the application of the neutral water cue (Fig. 1). TFS and control tadpoles were significantly less active than CFS tadpoles for brief periods (60 sec and 120 sec, respectively) prior to application of the water cue ($F_{2,252} > 8.29, P < 0.0001$; Fig. 1).

In contrast to the water cue, there were significant differences in swimming activity between tadpoles from different conditioning treatments after application of the sunfish cue ($F_{2,18} = 62.09, P < 0.0001$; Fig. 2). Tadpoles that had been conditioned in the TFS treatment were significantly more active than tadpoles that had been raised in the control (no predator)

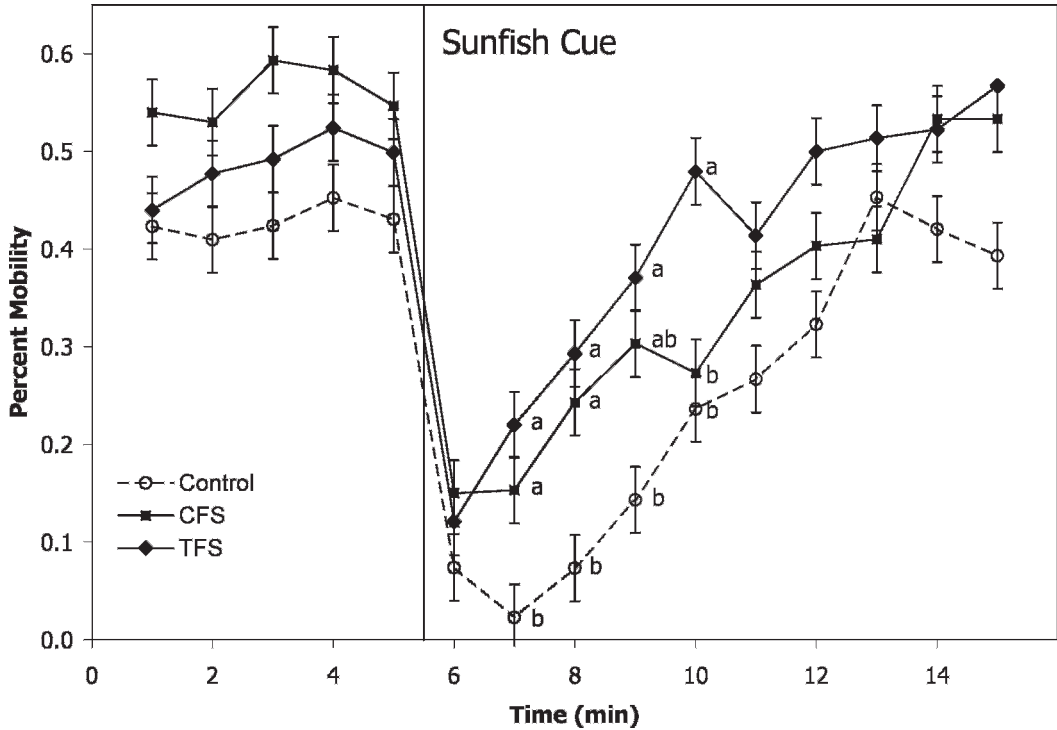


FIG. 2. Swimming activity (mean and SE of percent mobile during 1-min periods) of Lowland Leopard Frog *Lithobates (Rana) yavapaiensis* tadpoles previously exposed to control, cricket-fed sunfish (CFS), or tadpole-fed sunfish (TFS) conditioning treatments for 10 days. Each point is the mean of 10 replicates, each with five tadpoles. One liter of water with scent of Green Sunfish was applied after 5 min. Letters indicate time segments when swimming activity of tadpoles differed significantly between treatments after correction for multiple comparisons ($\alpha = 0.001$).

tanks between the sixth and 10th minutes of filming (i.e., 1–5 min after the sunfish cue was applied; $F_{2,252} > 8.96$, $P < 0.0001$). Similarly, tadpoles conditioned in the CFS treatment were significantly more active than control tadpoles for 2 min (between the first and third minutes after application of the cue; $F_{2,252} > 8.29$, $P < 0.0001$).

DISCUSSION

Our results indicate that the behavioral response of Lowland Leopard Frog tadpoles to the chemical scent of Green Sunfish is conditional on prior experiences. The differences in behavior resulting from conditioning treatment are short lived (2–4 min, starting 1 min after exposure to sunfish cue) but are still detectable 3–4 days after the conditioning period ended. These results are consistent with other recent studies that have demonstrated that tadpoles are capable of various forms of learning (Mandrillon and Saglio, 2005, 2007; Ferrari et al., 2007; Gonzalo et al., 2007).

Contrary to our expectations, tadpoles in the TFS and CFS treatments were significantly more active than control tadpoles in response to the sunfish cue (Fig. 2). Indeed, we had speculated that tadpoles that had previously witnessed sunfish predation events would be more likely to remain immobile in response to the sunfish cue. However, our results mirror those from a previous study (Griffiths et al., 1998) where Majorcan Midwife Toad *Alytes muletensis* tadpoles from ponds without snake predators (analogous to our control conditioning treatment) showed a much stronger decrease in swimming activity when exposed to the cues of a snake predator than tadpoles from a high snake predation pond (analogous to our TFS conditioning treatment).

We are uncertain why tadpoles from high-predation treatments show a weaker decrease in swimming activity in response to sunfish chemical cues than do control tadpoles. One possible explanation is that tadpoles may have become habituated to the presence of the sunfish during the 10-day conditioning period

during which the tadpoles repeatedly observed a sunfish predator through the transparent tank divider, but without being directly attacked (Holomuzki and Hatchett, 1994; Laurila et al., 2004). Alternatively, the repeated exposure to sunfish (CFS or TFS treatments) may increase overall tadpole swimming activity (before water cue is applied, see Fig. 1). Wilson et al. (2005) found that *Rana lessonae* tadpoles raised in the presence of Pumpkinseed Sunfish *Lepomis gibbosus* were significantly more active than control tadpoles, although the authors attribute the observed differences in swimming activity to induced differences in tail morphology. We did not measure tail morphology or the behavioral response of tadpoles when initially exposed to sunfish cues; hence, the heightened swimming activity in the CFS and TFS tadpoles could be the result of induced morphology, habituation, or a predator-induced behavioral response.

As anticipated, the response of tadpoles from the CFS conditioning treatment to the sunfish cue was intermediate to that of control and TFS treatments (Fig. 2). Overall, the behavioral response of tadpoles in the two sunfish conditioning treatments largely paralleled one another. Our interpretation of these results is that, although an alarm cue (i.e., tadpole prey) is not necessary for learning to occur, the cue appears to reinforce learning (Semlitsch and Reyer, 1992; Mirza et al., 2006).

A review of the studies that have documented learning in tadpoles reveals an apparent qualitative difference between alarm cues that are naturally produced (when allowing predators to feed on tadpoles) and experimentally (by grinding tadpole tissue). Indeed, studies in which tadpole learning has been described generally have used experimentally produced alarm signals (Mandrillon and Saglio, 2005; Ferrari et al., 2007; Gonzalo et al., 2007). Although the metabolites of predators that were previously fed tadpoles are sufficient to induce a morphological response in tail shape in focal tadpoles (e.g., LaFiandra and Babbitt, 2004), we are aware of only a single study (Mandrillon and Saglio, 2007) besides this one where tadpoles modified their behavior as a result of witnessing the predation of conspecifics in the absence of experimentally produced alarm cues. Furthermore, in a study that included both tadpole-fed predators and experimentally ground tadpoles as sources of alarm signals, only the latter induced a learned response in focal tadpoles (Mandrillon and Saglio, 2005). Collectively, these studies suggest that concentrations of alarm cues may often be too low for learning to occur in tadpoles (Mirza et al., 2006) and raise the question of whether there may be

strong selection in predators to minimize the production of alarm cues during prey consumption, digestion, and excretion.

Although we have demonstrated that Lowland Leopard Frog tadpoles altered their behavior in response to prior exposure to Green Sunfish, it remains to be tested whether this induced behavior is adaptive in the wild. Furthermore, we cannot confidently conclude that Lowland Leopard Frog tadpoles are capable of learning any nonnative predator. To do so would require that we demonstrate that the observed change in swimming activity was induced specifically by Green Sunfish scents and not simply a response to a novel cue (although both may be potentially adaptive, Kats and Dill, 1998). Additionally, we would need to sample a greater number of native and nonnative predators to distinguish between a species-specific response and a generalized response to a fishlike organism. Nevertheless, the observed response indicates at least the potential of Lowland Leopard Frogs to alter their swimming behavior in response to some nonnative predators.

Understanding the proximate mechanisms underlying predator-prey interactions between species without a shared evolutionary history is important for conservation biology because native prey are often naïve to the threat of novel predators, especially in aquatic environments (Schlaepfer et al., 2005; Cox and Lima, 2006; Salo et al., 2007). This study has potentially important implications for the conservation of native prey species because it suggests that, in some instances, normal predator-avoidance behaviors can be coopted for novel situations. Future studies should investigate whether native prey are biased in their ability to learn in favor of evolutionarily familiar predators and then test the extent to which induced responses are adaptive under different ecological circumstances.

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