# The use of chemical cues in predator recognition by western toad tadpoles

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**Abstract.** Western toad, *Bufo boreas*, tadpoles were collected from a lake in the Cascade Mountains of central Oregon, where they occur in sympatry with backswimmers, *Notonecta* spp., giant waterbugs, *Lethocerus americanus*, common garter snakes, *Thamnophis sirtalis*, roughskin newts, *Taricha granulosa* and rainbow trout, *Oncorhynchus mykiss*. Backswimmers, waterbugs and snakes prey on toad tadpoles. Newts and trout are potential tadpole predators, but they find toad tadpoles unpalatable. In laboratory tests, groups of tadpoles responded with anti-predator behaviour when exposed to live backswimmers, waterbugs and snakes, but not when exposed to either newts or trout. In subsequent tests, when only chemical cues from the stimulus animals were presented, the toad tadpoles again responded to backswimmers, waterbugs and snakes, but not to either newts or trout. When tests were conducted using only visual cues, tadpoles did not respond with anti-predator behaviour to any of the heterospecifics with the possible exception of garter snakes. These results show that western toad tadpoles can distinguish between predatory and non-predatory heterospecifics with which they co-occur, and that predator recognition by toad tadpoles is primarily based on chemical cues.

The failure of a prey animal to recognize and respond to a predator increases the probability that it will be captured during an encounter with a predator. A prey animal that gives an anti-predator response upon encountering a non-predator, however, wastes valuable time and energy that would otherwise be available for other activities such as foraging and reproduction (Lima & Dill 1990). As a result, there should be strong selection pressure on prey to distinguish between predatory and non-predatory species. In a series of laboratory experiments, we examined the ability of western toad tadpoles, *Bufo boreas*, to distinguish between different classes of heterospecifics with which they co-occur.

Western toad tadpoles, like other bufonids, contain bufotoxin (bufondienolides: Flier et al. 1980) in their skin. These chemicals make tadpoles unpalatable to many predators (e.g. Voris & Bacon 1966; Wassersug 1971; Cooke 1974; Walters 1975; Brodie et al. 1978; Formanowicz &

Brodie 1982). Predators that swallow tadpoles whole, or invertebrate predators that pierce the skin and suck body fluids, are less affected by tadpole chemical defences than predators that masticate, bite or somehow taste the tadpoles (e.g. Kruse & Stone 1984; Peterson & Blaustein 1992). At one of our field sites in the Cascade Mountains of Central Oregon, we have observed three species that readily prey on toad tadpoles: two invertebrates, the backswimmer, *Notonecta* spp., and the giant waterbug, *Lethocerus americanus*, and one vertebrate, the common garter snake, *Thamnophis sirtalis*. Each of these predators readily consumes toad tadpoles under both laboratory and field conditions (Arnold & Wassersug 1978; Hews 1988; Nussbaum et al. 1988; Peterson & Blaustein 1992). Two additional species found at our study site, roughskin newts, *Taricha granulosa*, and rainbow trout, *Oncorhynchus mykiss*, are potential predators on toad tadpoles, but they find toad tadpoles unpalatable (Peterson & Blaustein 1991; J. Kiesecker & A. Blaustein, unpublished data). Peterson & Blaustein (1991) documented that western toad tadpoles are typically expelled shortly after capture by newts; however, under laboratory conditions some newts may feed on

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toad tadpoles if the newts are starved for several days. Bufonid tadpoles are generally unpalatable to fish predators (Voris & Bacon 1966; Kruse & Stone 1984; Kats et al. 1988). Western toad tadpoles, specifically, are unpalatable to various salmonid species, including rainbow trout (J. Kiesecker & A. Blaustein, unpublished data).

In our experiments, we tested whether toad tadpoles would show anti-predator behaviour in response to backswimmers, giant waterbugs and garter snakes, but not in response to newts and trout. We also investigated the specific sensory modality used by the tadpoles in responding to stimuli from predators. Numerous studies have shown that larval amphibians respond specifically to chemical stimuli from potential predators in the absence of visual stimuli. (e.g. Petranka et al. 1987; Kats 1988; Elliott et al. 1993; Feminella & Hawkins 1994; Lefcort 1996). Most studies of chemosensory-based anti-predator responses among amphibians have used stimuli from vertebrate predators, but few studies have used stimuli from invertebrate predators, or tested for responses of amphibians to visual stimuli from predators in the absence of chemical cues (but see Stauffer & Semlitsch 1993). In our experiments, we tested whether toad tadpoles respond to each of the five heterospecifics when we provided chemical stimuli alone, visual stimuli alone and a combination of visual and chemical stimuli.

## METHODS

### Collection and Maintenance

Western toad tadpoles were collected from Lost Lake (Linn County, Oregon, 97 km east of Albany, Oregon), and transported to our laboratory for testing. Tadpoles were maintained in 38-litre aquaria on a 14:10 h light:dark photoperiod at approximately 15–20°C. Tadpoles were fed ad libitum with rabbit chow.

All stimulus animals (backswimmers, giant waterbugs, common garter snakes, roughskin newts and rainbow trout) used in experiments are found at Lost Lake. With the exception of the rainbow trout, which were obtained from a fish hatchery, all stimulus animals were collected from Lost Lake and other nearby lakes where toad tadpoles are found. Like the tadpoles, the stimulus animals were maintained on a 14:10 h L:D photoperiod at approximately 15–20°C.

Chemosensory-based anti-predator responses among predator-naive fishes (Mathis & Smith 1993), amphibians (Wilson & Lefcort 1993) and insects (Chivers et al. 1996) may be influenced by the predator's recent diet; i.e. anti-predator responses may be elicited only if the predators have recently fed on the prey's conspecifics. Due to the short duration of our experiments (15–26 July 1994), we did not feed the stimulus animals during the experiments. Given that we collected our stimulus animals from an area containing toad tadpoles, it is possible that the stimulus animals had recently fed on toad tadpoles. Consequently, we are unsure whether dietary cues were important in our studies.

### Experiment 1: Response to Visual and Chemical Cues

In this experiment, we tested whether toad tadpoles responded to the presence of a potential predator when exposed to both chemical and visual cues of that animal. We tested tadpoles in a rectangular aquarium (100 × 60 cm) with opaque walls. A line divided the tank into width-wise halves and fibreglass screen was placed across both ends of the tank creating a 25 × 60 cm cage at each end of the tank. We thoroughly rinsed the tank with tap water before each test and filled it with dechlorinated tap water to a depth of 10 cm. Five test animals were simultaneously placed in a central cage (9 cm diameter) and allowed to acclimate for 10 min. During control tests, both of the end cages were empty. During experimental trials one of the end cages ('predator compartment') contained the stimulus animal(s). Stimulus animals were placed in the predator compartment 40 min prior to the start of each test.

A test began after the 10-min acclimation period, when the centre cage was lifted, releasing the tadpoles. Each test included two 5-min trials (an initial and a final response) separated by a 5-min pause. An observer concealed behind an opaque blind measured tadpole activity and distribution. As a measure of activity level, we counted the number of times any of the five tadpoles crossed the centre line during each trial. To assess avoidance of the predator compartment, we counted the number of test individuals on each end of the tank at 30-s intervals. These 30-s counts were then averaged for each test. We randomly altered the position of the stimulus animals from

end to end for each test within a treatment, and the treatments were presented in random order. We considered each group of five tadpoles as a single replicate and had 10 replicates of each treatment ($N=60$ tests). Test individuals were never used in more than one test.

## Experiment 2: Response to Visual Cues Alone

In this experiment, we tested whether groups of tadpoles would respond to each of the heterospecifics when exposed to only visual cues. Testing took place in a manner identical to experiment 1, except that 6.25-mm thick glass, instead of a fibreglass screen, was used to create the end cages. Thus, test animals were only exposed to visual cues of stimulus animals. Again we had 10 replicates of each treatment ($N=60$ tests). Test individuals were never used in more than one test.

## Experiment 3: Response to Chemical Cues Alone

In this experiment, we tested whether groups of toad tadpoles would respond to the presence of each of the heterospecifics when exposed to only chemical cues. We tested tadpoles in a gravitational flow-through system (modified from Petranka et al. 1987) composed of three 25-litre plastic tubs measuring $51 \times 37 \times 21$ cm deep. The tubs were placed at different heights so that water flowed from one to another at 0.6 litres/min. The two lower-most tubs had both input and output openings and never contained more than 12 litres of water. The upper container was filled with 23 litres of water. We added stimulus animals to the middle tub 40 min prior to the start of each test. From the middle tub, water flowed to the lower-most tub, which contained five tadpoles and which was marked with a line that divided the tank into width-wise halves. A shelter made of opaque Plexiglas ($25 \times 37$ cm) was present on the output side of the lower tank. The water in the lower tank was 10 cm deep. The shelter was placed at a depth of 5 cm; thus, tadpoles had a choice of swimming above or below the shelter.

A test began 10 min after the flow was initiated. Each test included two 5-min trials separated by a 5-min pause. An observer concealed behind an opaque blind measured tadpole activity and distribution. As a measure of activity level, we counted the number of times a test animal crossed the centre line during each trial. We also counted the number of test individuals under the shelter at 30-s intervals. These 30-s counts were then averaged for each test. The treatments were presented in random order. Again we had 10 replicates of each treatment ($N=60$ tests). Test individuals were never used in more than one test.

For all experiments, stimulus animals used in tests were arbitrarily drawn from stock tanks and then returned after testing. Within a given treatment, all animals were size-matched between tests ($\bar{X} \pm$ SE total length: backswimmers= $1.73 \pm 0.23$ cm; giant waterbugs= $4.37 \pm 0.41$ cm; common garter snakes= $43.47 \pm 2.57$ cm; rough-skin newts= $17.7 \pm 3.24$ cm; rainbow trout= $15.5 \pm 1.6$ cm). In all tests except the backswimmer tests, a single stimulus animal was used. Owing to the small size of backswimmers, three individuals were used in all tests. The tadpoles used were all of the same developmental stage (Gosner stage 25; Gosner 1960) and approximate size (total length= $3.67 \pm 0.28$ cm).

## Statistical Analyses

For all three experiments, we summed the number of times tadpoles crossed the centre line during the initial and final 5-min of each test. For experiments 1 and 2, we calculated the mean number of individuals away from the predator compartment (arbitrarily determined for control treatments) for each 30-s reading during the initial and final 5-min of each test. For experiment 3, we calculated the mean number of individuals under the shelter for each 30-s reading during the initial and final 5-min of each test. For each experiment, we initially tested whether there was a difference in the tadpoles' initial responses (first 5 min) and final responses (last 5 min) using $t$-tests. Because there was no difference between the initial and final responses in any of the experiments ($P>0.37$ for all comparisons) the data from initial and final responses were combined for further analyses. We then used multivariate analysis of variance (MANOVA) to test for stimulus effects (Tabachnick & Fidell 1989). After MANOVA, we used univariate analysis of variance (ANOVA) on each response variable to assess which variables were responsible for significant main effects. Post hoc comparisons (Tukey tests) were performed to test for differences between means among the stimuli presented (Zar 1984). For all experiments,

**Table I.** Results of MANOVA for overall effects on stimulus type on tadpole behaviour and ANOVAs for each response variable

|                          | $F^1$    | $P$      |
| ------------------------ | -------- | -------- |
| **Experiment 1 (Chemical and visual cues)** |          |          |
| MANOVA                   | 390.67   | <0.001   |
| ANOVAs                   |          |          |
|   Activity     | 70.36    | <0.001   |
|   Side         | 65.77    | <0.001   |
| **Experiment 2 (Visual cues)** |          |          |
| MANOVA                   | 137.54   | <0.001   |
| ANOVAs                   |          |          |
|   Activity     | 10.56    | <0.01    |
|   Side         | 0.118    | 0.214    |
| **Experiment 3 (Chemical cues)** |          |          |
| MANOVA                   | 225.40   | <0.001   |
| ANOVAs                   |          |          |
|   Activity     | 51.32    | <0.001   |
|   Shelter      | 80.70    | <0.001   |

Response variables are number of times a tadpole crossed the centre line (activity) and the number of tadpoles counted away from the predator compartment (side), for experiments 1 and 2, or the number of tadpoles under the shelter (shelter), for experiment 3. Significance level for univariate tests is 0.025 (Bonferroni-adjusted for two response variables).
[1]Degrees of freedom are 12, 106 for MANOVAs and 5, 54 for ANOVAs.

parametric assumptions were met and no data transformations were necessary.

## RESULTS

### Experiment 1: Response to Visual and Chemical Cues

A MANOVA revealed that the type of hetero-specific presented in the predator compartment affected tadpole behaviour (Table I). Subsequent ANOVAs showed that both activity (number of centre-line crosses) and use of the area near the predator compartment was significantly affected by the type of heterospecific presented (Table I). Multiple comparisons revealed that tadpoles reduced their activity and spent significantly less time near the predator compartment in response to backswimmers, giant waterbugs and garter snakes when compared to the controlled treatment (Tukey HSD, $P<0.01$ for all comparisons; Fig. 1). There was no difference between the control treatment and either the newt or trout

treatment in terms of activity or use of the area near the predator compartment (Tukey HSD, $P>0.50$ for all comparisons; Fig. 1).

### Experiment 2: Response to Visual Cues Alone

A MANOVA revealed that the type of hetero-specific presented in the end compartment affected tadpole behaviour (Table I). Subsequent ANOVAs showed that activity but not use of the area near the predator compartment was significantly affected by the type of heterospecific presented (Table 1). Multiple comparisons revealed that, when compared to the control treatment, tadpoles reduced activity in response to garter snakes (Tukey HSD, $P<0.01$; Fig. 2). There was no difference between activity in the control treatment and any of the other heterospecific treatments (Tukey HSD, $P>0.50$ for all comparisons; Fig. 2).

### Experiment 3: Response to Chemical Cues Alone

The results of experiment 3 closely correspond to those of experiment 1. A MANOVA revealed that the type of heterospecific cue presented affected tadpole behaviour (Table I). Subsequent ANOVAs revealed that both activity and use of the shelter was significantly affected by the type of heterospecific presented (Table I). Multiple comparisons revealed that tadpoles reduced their activity and use of shelter in response to back-swimmers, giant waterbugs and garter snakes when compared to the control treatment (Tukey HSD, $P<0.01$ for all comparisons; Fig. 3). There was no difference between the control treatment and either the newt or trout treatment in terms of activity or use of the shelter (Tukey HSD, $P>0.50$ for all comparisons; Fig. 3).

## DISCUSSION

These results show that western toad tadpoles show anti-predator behaviour in response to three natural predators (backswimmers, giant water-bugs and common garter snakes), but not in response to two potential predators (rainbow trout and roughskin newts) that find them unpalatable. The anti-predator responses included a reduction in movement, avoidance of the predator compartment and an increase in shelter
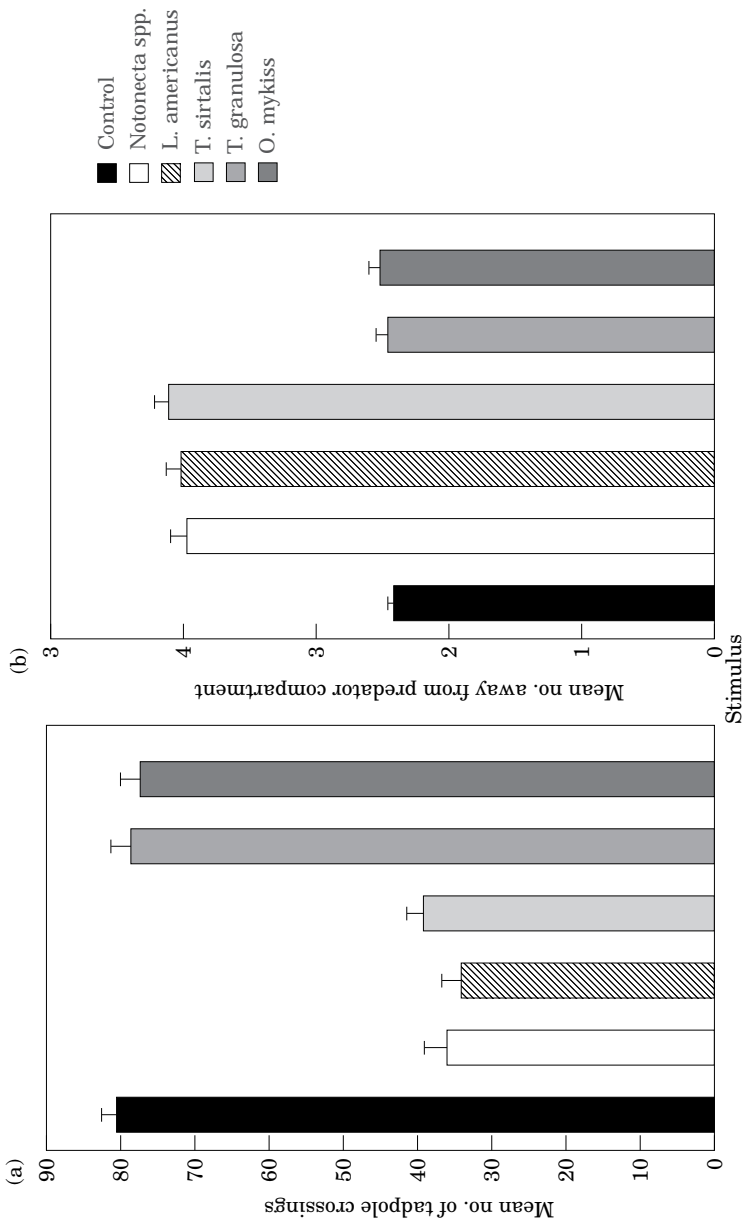
**Figure 1.** Mean+SE (a) number of tadpole crossings and (b) number of individuals away from the predator compartment for tadpoles exposed to both chemical and visual cues of stimulus animals, based on 10 replicates for each treatment.
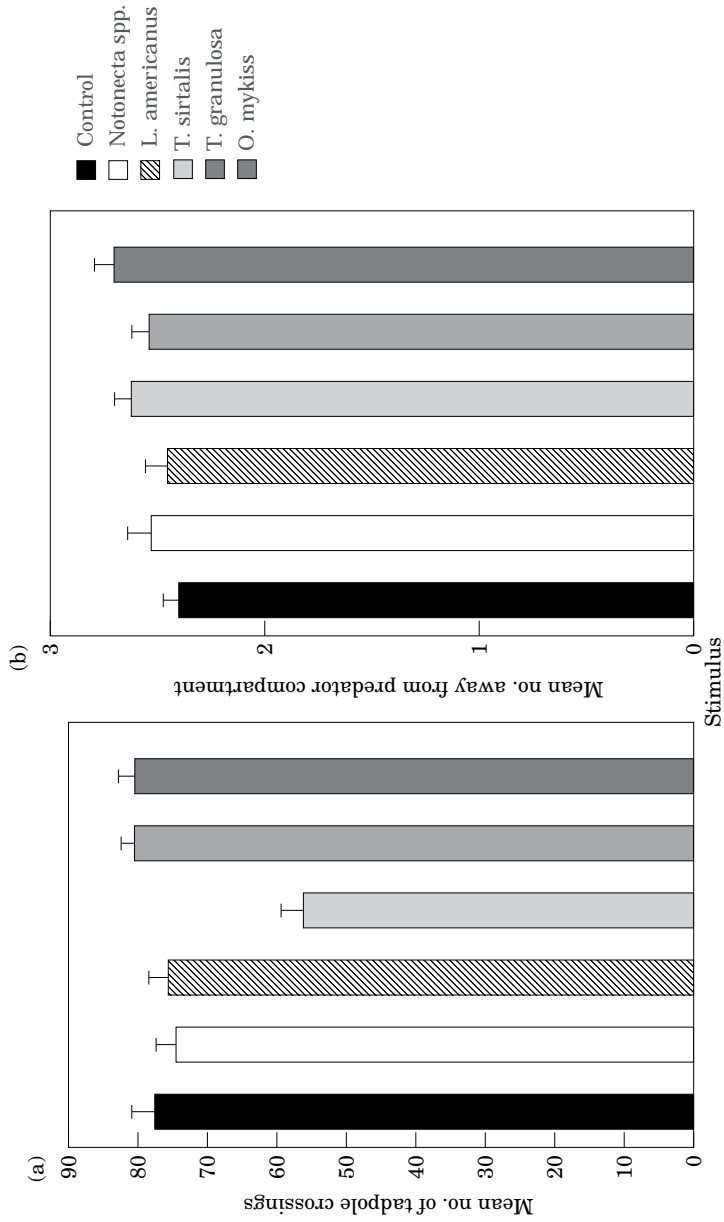
**Figure 2.** Mean+SE (a) number of tadpole crossings and (b) number of individuals away from the predator compartment for tadpoles exposed to only visual cues of stimulus animals, based on 10 replicates for each treatment.
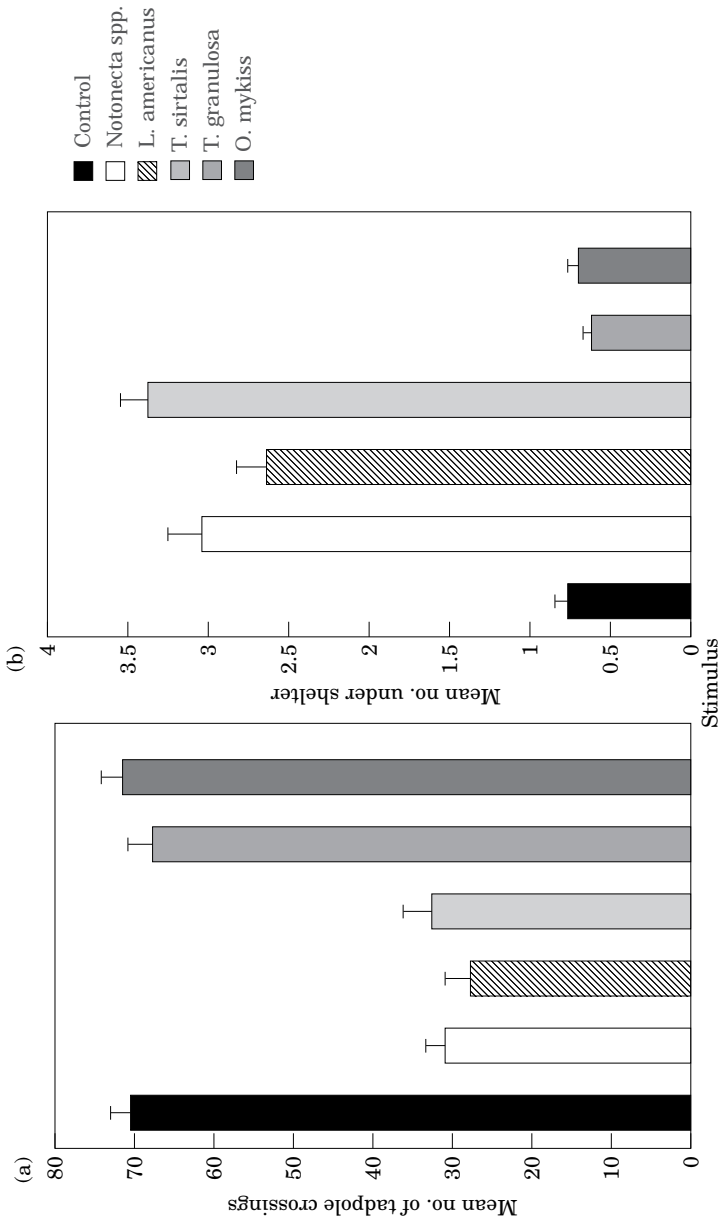
**Figure 3.** Mean+SE (a) number of tadpole crossings and (b) number of individuals under shelter for tadpoles exposed to only chemical cues of stimulus animals, based on 10 replicates for each treatment.

use. All of these responses are commonly reported responses of prey to the presence of predators (Sih 1987; Lima & Dill 1990). Decreased movement and increased shelter use may be particularly adaptive against predators that locate their prey through detecting the prey's movement.

Given that we used wild-captured tadpoles in our experiments, we do not know whether the ability of tadpoles to recognize predators is a result of experience or genetic factors. Kats et al. (1988; see also Sih & Kats 1994) found that several larval amphibians, collected as eggs from ponds that contain predatory fish, showed an increase in shelter use when exposed to chemical cues from green sunfish, *Lepomis cyanellus*, even in the absence of experience with sunfish. In contrast, other studies have indicated that experience may be important for predator recognition in amphibians (e.g. Semlitsch & Ryer 1992). Further work is needed to differentiate between experience and genetic factors in predator recognition by western toad tadpoles.

Our experiments demonstrate the ability of toad tadpoles to recognize predators using only chemical cues. Many vertebrates, including many species of amphibians, recognize predators through chemical stimuli (Weldon 1990; Dodson et al. 1994). Chemical stimuli may provide aquatic animals with critical information, especially at night, in turbid water or in highly structured habitats when visual information is not available. Moreover, detection of predators through chemical stimuli may be critical for detecting cryptic ambush predators.

Chemosensory predator recognition seems to be particularly important for western toad tadpoles because they do not appear to visually recognize at least some of their predators. In our experiment, toad tadpoles did not respond to the sight of either backswimmers or giant waterbugs. Experiment 2 showed that toad tadpoles did respond to the sight of the garter snakes (in terms of decreased activity). However, during the trials we noted that backswimmers, giant waterbugs, newts and trout remained relatively motionless, but the snakes were very active in the tanks. Therefore, the response of toad tadpoles to visual stimuli from snakes may have represented recognition of a disturbance caused by the sight of the movement of the snakes and not recognition of the predator per se. The importance of chemosensory (and not visual) cues in predator recognition

by toad tadpoles is consistent with findings from other amphibians. Stauffer & Semlitsch (1993), for example, showed that two species of tadpoles, *Rana lessonae* and *R. esculenta*, responded more intensely to the odour than to the sight of a northern pike, *Esox lucius*. Other studies have also shown that chemical (and not visual) cues are important in other aspects of amphibian ecology. For example, anuran larvae recognize kin based on chemosensory but not visual cues (Blaustein & O'Hara 1982; Dawson 1982; Waldman 1985; Blaustein et al. 1993). Further experiments are needed to assess the importance of chemosensory versus visual information in predator/prey interactions in other aquatic taxa.

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