

EXPERIENCE HAS NO EFFECT ON THE DEVELOPMENT OF CHEMOSENSORY RECOGNITION OF PREDATORS BY TADPOLES OF THE AMERICAN TOAD, *BUFO AMERICANUS*

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ABSTRACT: Although chemosensory recognition of predators by larval amphibians is well known, the extent to which experience plays a role in the development of this anti-predator behavior is unclear. We addressed this issue by exposing laboratory-reared (naive) and wild-caught (experienced) tadpoles of the American toad, *Bufo americanus*, to water-borne chemical cues of three different potential predators (bluegill sunfish, *Lepomis macrochirus*, larvae of the odonate *Anax junius*, and adults of the red-spotted newt, *Notophthalmus viridescens*). Compared to control tadpoles exposed to dechlorinated water, tadpoles exposed to chemical cues of *Lepomis* and *Anax* significantly decreased activity and significantly increased aggregation. However, the behavior of tadpoles exposed to chemical cues of *Notophthalmus* was identical to that of control tadpoles. Most importantly, we found no difference in anti-predator behavior between laboratory-reared and wild-caught tadpoles. We conclude that larval experience with predators is unnecessary for the development of chemosensory predator recognition and that anti-predator behavior in this species is largely innate.

Key words: Anti-predatory behavior; Tadpoles; *Bufo americanus*; Chemical cues; Chemosensation; Predator recognition; *Anax*; *Lepomis*; *Notophthalmus*

CHEMOSENSATION, the ability to detect and recognize chemical cues produced by other organisms, mediates virtually all aspects of the behavior of larval amphibians, especially predator detection and avoidance. Larval amphibians perform a variety of anti-predator behaviors in response to chemical cues from both predators (Griffiths et al., 1998; Holomuzki, 1995; Kiesecker et al., 1996; Laurila et al., 1997; Lefcort, 1998; Petranka and Hayes, 1998; Semlitsch and Reyer, 1992; Skelly and Werner, 1990) and damaged tissues of conspecifics (Chivers et al., 1996; Wilson and Lefcort, 1993). Some species of larval amphibians form aggregations for defense in response to chemicals cues from predators, and also use chemosensation in kin recognition when forming aggregations (Watt et al., 1997). Tadpoles respond to chemical cues from actual predators and have minimal if any response to chemical cues from non-predatory species (Kiesecker et al., 1996; Lefcort, 1996; Semlitsch and Reyer, 1992).

Although tadpole chemosensory recognition of predators has been studied extensively, it is not clear what role larval experience plays in the development of

predator recognition and anti-predatory behavior. Some studies have found that previous experience with predators has a significant influence on the development of amphibian anti-predatory behavior (Bridges and Gutzke, 1997; Semlitsch and Reyer, 1992), and similar results have also been obtained using fish (Magurran, 1990; Mathis et al., 1996). Other studies of amphibians, however, have found that previous experience with predators has no effect on subsequent chemosensory recognition and avoidance of predators (Laurila et al., 1997; Sih and Kats, 1994).

Our study addresses the issue of previous experience and the development of predator recognition in tadpoles of the American toad, *Bufo americanus*. We evaluated the ability of American toad tadpoles to detect and respond to the chemical cues of three potential predators (larvae of the odonate *Anax junius*, the bluegill sunfish, *Lepomis macrochirus*, and the red-spotted newt, *Notophthalmus viridescens*), and compared laboratory-reared and wild-caught tadpoles to determine the role of larval experience in the development of predator recognition and anti-predatory behavior. Although tadpoles of *Bufo* are

relatively unpalatable to some predators (Kats et al., 1988; Kiesecker et al., 1996), larvae of *Anax junius* are voracious predators on tadpoles of *Bufo* (Anholt et al., 1996; Petranka and Hayes, 1998; Skelly and Werner, 1990; Van Buskirk and Yurewicz, 1998), and species of *Lepomis* are known to prey upon tadpoles of *Bufo* as well (Holomuzki, 1995). *Notophthalmus viridescens* preys on eggs of *Bufo* and small larvae, but because of limited gape size, it is unable to prey on larger tadpoles (Lawler, 1989; Petranka et al., 1994; Wilbur and Fauth, 1990; Wilbur et al., 1983). All three species live sympatrically with American toads over much of eastern North America, so our experiments should reflect ecological conditions that exist commonly in nature.

METHODS

Our study was conducted in Crawford County in northwestern Pennsylvania, USA. In this region, *Bufo americanus* breeds across a range of temporary and permanent wetlands, including ponds with and without predatory fish. Eggs and tadpoles of *Bufo* used in our study were obtained from a small (1 ha) permanent pond 10 km east of Meadville. Two of the three species of potential predators used in our study occur in the same pond. *Lepomis* is abundant there, *Anax* is also present but only at very low densities, and *Notophthalmus* is absent.

On 6 May 1998, we collected four egg strings (clutches) of *B. americanus* from the pond and housed them in the laboratory in 36-l tanks containing dechlorinated water, 1 cm of gravel, a filter, and an air stone. Eggs began hatching on 8 May. These laboratory-reared tadpoles comprised the naive treatment and were reared in isolation from heterospecifics. We collected wild-caught tadpoles from the same permanent pond on 18 May, 10 days after eggs first began hatching; they comprised the experienced treatment and had been exposed to a variety of heterospecifics, including *Lepomis* (abundant in the pond), and *Anax* (rare) but not *Notophthalmus* (absent). Both treatments comprised mixed sibships. In the labora-

tory, both naive and experienced tadpoles were housed under the same conditions with a natural photoperiod (15 h light, 9 h dark) and at a consistent water temperature of 23 C. We fed the tadpoles a diet of rabbit chow.

We had collected *Lepomis* several months earlier from the same permanent pond from which eggs and tadpoles of *Bufo* were collected. Because *Anax* was present only at very low densities there and *Notophthalmus* was absent, we collected these predators from four small temporary ponds at the Allegheny College Environmental Research Reserve (Wissinger and Gallagher, 1999), 10 km southeast of Meadville (larval *Bufo* were also present in these temporary ponds, but *Lepomis* was absent). Both *Anax* and *Notophthalmus* were collected on 18 May. To assure the predatory status of each of the potential predators, we conducted preliminary predation trials with the three species of potential predators on 20 May. *Lepomis* and *Anax* readily consumed tadpoles of *Bufo*, but *Notophthalmus* did not. Because the duration of our study was short, we did not subsequently feed stimulus organisms during experimental testing, thereby avoiding complications that could be introduced by variation in predator diet (Kiesecker et al., 1996; Wilson and Lefcort, 1993).

Experimental Procedures

We performed trials in which laboratory-reared and wild-caught tadpoles were exposed to water-borne chemical cues of the three potential predators. We also conducted control trials in which tadpoles from both rearing treatments were exposed to dechlorinated water. Overall, there were eight treatment groups in a 2 × 4 factorial design and 10 replicates of each treatment ($n = 80$ trials).

Our experimental setup and procedure were similar to those of Kiesecker et al. (1996) and Wilson and Lefcort (1993). We used a gravitational flow-through system as the testing apparatus. This apparatus consisted of three tubs at different heights that enabled water to travel through plastic tubing from one tub into another below.

Water was siphoned from the top (stimulus) tub ($23 \times 15 \times 16.6$ cm) that contained the stimulus organisms, dechlorinated tap water (5 l), and gravel. The water then traveled into the middle (testing) tub ($30 \times 16 \times 8$ cm) containing the test tadpoles and dechlorinated water (1 l). Water was then siphoned out of the middle tub into another tub at the same rate at which water flowed into it (approximately 0.9 l/min). Water that flowed out of the middle tub was manually recycled back into the top tub so that the system flowed continuously. To ensure that chemical cues were present in the stimulus water, we housed *Anax* ($n = 5$: 3.5–5.0 cm) and *Notophthalmus* ($n = 5$: 8.3–9.7 cm) in the same tubs that served as the respective stimulus tubs. Each of the five *Anax* and five *Notophthalmus* were used in all of the trials. Because of their large size, however, individuals of *Lepomis* ($n = 2$: 7.5–7.9 cm) were housed in a 36-l tank. Twenty minutes prior to testing, we placed one *Lepomis* (randomly chosen) into a stimulus tub identical to that of the tubs used by the other organisms.

The testing tub contained an opaque semi-circular shelter 8 cm in diameter and 1.8 cm tall. The bottom of the tub was marked with a line that divided it in half (width-wise). We used five tadpoles in each of the 80 trials. The tadpoles were given a 5-min acclimation period in the testing tub (Griffiths et al., 1998). After acclimating, the water flow was initiated and data collection began after an additional 2-min acclimation period had elapsed. We allowed the additional 2-min acclimation period so that the tadpole's initial reaction to the flowing water would not be included in the data collection. During the experiment, an observer was concealed behind an opaque blind while monitoring tadpole activity and distribution. Data collection lasted for 10 min (Griffiths et al., 1998; Kats et al., 1988). The trials were performed as randomized blocks. A block consisted of a replicate of all eight treatments in random order. In all, 10 complete blocks were performed. Block testing eliminated any biases that development stage may have caused. Gosner (1960)

stages ranged from 24–25 during block 1 to 27–29 during block 10 and did not differ between laboratory-reared and wild-caught tadpoles.

We conducted tests from 22–30 May 1998 and recorded three tadpole anti-predatory behaviors. A decrease in activity is a common anti-predatory behavior of toad tadpoles (Griffiths et al., 1998; Holomuzki, 1995; Kiesecker et al., 1996; Laurila et al., 1997; Lefcort, 1998; Petranka and Hayes, 1998; Semlitsch and Reyer, 1992; Skelly and Warner, 1990; Van Buskirk and Yurewicz, 1998; Wilson and Lefcort, 1993), and we measured it as the number of times that the five test tadpoles crossed the center line. We recorded shelter usage (Holomuzki, 1995; Kiesecker et al., 1996; Lefcort, 1998; Semlitsch and Reyer, 1992) by counting the number of tadpoles present within the shelter at 1-min intervals. We then averaged the counts for the entire 10-min trial. The third anti-predator behavior that we recorded was the formation of aggregations (Watt et al., 1996). A grid consisting of 12 rectangles (7×5.5 cm each) was drawn on the bottom of the testing tub. After 5 min and at the end of the 10-min testing period, for each tadpole we counted the number of other tadpoles within the same rectangle. Thus, if all five tadpoles were in different rectangles, the aggregation index score would be zero for each tadpole. If all five tadpoles were in the same rectangle, the aggregation index score would be four for each tadpole. The mean aggregation scores at the 5- and 10-min marks were then averaged for a final aggregation index.

Finally, after each experimental trial, we removed the tadpoles from the tub and placed them in a separate tank. No tadpole was used in more than one trial. After removing all the organisms, the water in the testing tub was discarded and refilled with fresh dechlorinated water so that the chemical cues of the previous experiment would not affect subsequent trials that used different stimulus organisms.

Statistical Analyses

Because the three response variables were highly correlated, we followed Kie-

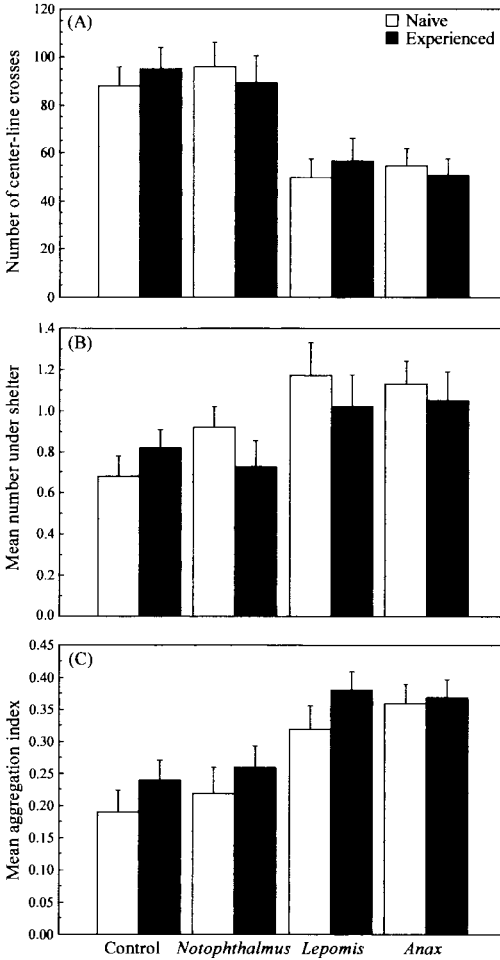


FIG. 1.—(A) Number of tadpoles crossing the center line, (B) mean number of tadpoles present under the shelter, and (C) mean aggregation index of tadpoles when presented with four different chemical stimuli. Error bars represent 1 SE.

gregation was significantly higher in the treatments with *Lepomis* and *Anax* than in the *Notophthalmus* and control treatments (all values of $P < 0.01$; Fig. 1), but no significant differences were detected in the comparisons between *Lepomis* and *Anax* ($P = 0.96$) or between *Notophthalmus* and the control ($P = 0.85$).

Tadpole development stage, as measured by experimental block, had significant effects on the number of center-line crosses and aggregation index, but not shelter use (Table 1, Fig. 2). The number of center-line crosses generally increased

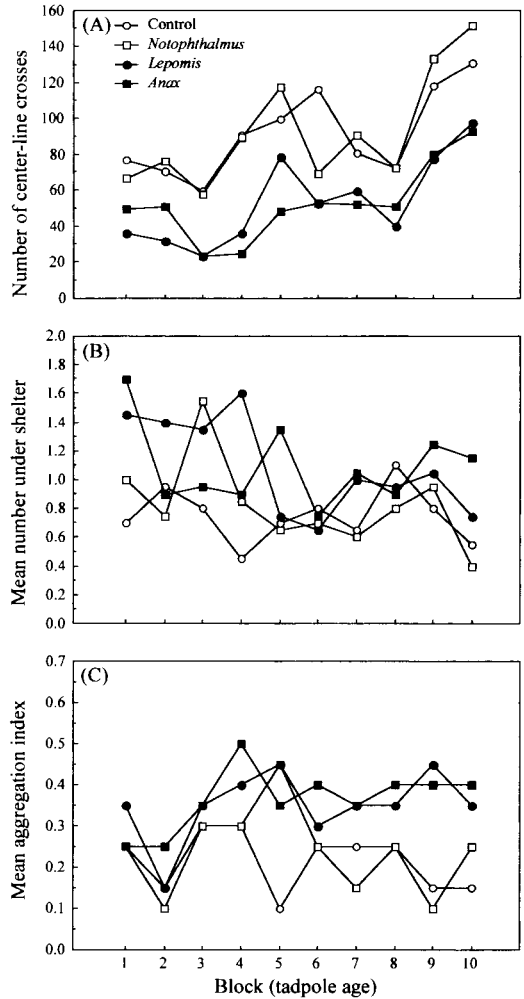


FIG. 2.—The effects of block (development stage of the tadpole) on (A) number of tadpoles crossing the center line, (B) mean number of tadpoles present under the shelter, and (C) mean aggregation index of tadpoles when presented with four different chemical stimuli. Each point represents the mean of two trials, one with laboratory-reared tadpoles and one with wild-caught tadpoles.

with tadpole age (Fig. 2). The relationship between age and mean aggregation index was more difficult to interpret and no clear pattern was evident (Fig. 2).

DISCUSSION

We found that tadpoles of *Bufo americanus* exhibited anti-predatory behavior in response to chemical cues of two known predators. These results are similar to

those obtained by other researchers working either on *B. americanus* (Petranka and Hays, 1998) or other members of the genus (Kiesecker et al., 1996). However, we also found that the anti-predatory responses of naive (laboratory-reared) tadpoles were essentially identical to those of experienced (wild-caught) tadpoles (Fig. 1); we found no significant effect of rearing treatment on any of the anti-predator behaviors (Table 1). In contrast to our results, Semlitsch and Reyer (1992) found that tadpoles of *Rana lessonae* and *R. esculenta* conditioned with predator chemical cues increased the occurrence of certain anti-predatory behaviors. Bridges and Gutzke (1997) also found that conditioning affected anti-predatory behavior of tadpoles, but in the opposite fashion; tadpoles of the gray treefrog, *Hyla chrysoscelis*, that were reared in the presence of predatory fish and crayfish apparently became habituated to these chemical cues and showed a reduction in anti-predatory behavior in response to these cues during experimental trials.

Tadpoles from both rearing treatments did not alter their behavior when presented with the chemical cues of *Notophthalmus*. *Notophthalmus* is known to prey on eggs of *Bufo* and small larvae, but because of limited gape size, it is unable to prey on larger tadpoles (Lawler, 1989; Wilbur and Fauth, 1990; Wilbur et al., 1983). At the time that we began our experimental trials, the tadpoles were approximately 14 days old (Gosner stages 24–25; Gosner, 1960) and may have been too large for *Notophthalmus*. This was confirmed with tests conducted immediately before our experimental trials in which 12-day old (Gosner stage 23) tadpoles of *Bufo* were placed in the same container as *Notophthalmus* and no predation occurred.

It is possible that response to the three types of potential predators was mediated by predator diet and response to alarm substance in the fecal matter or skin secretions of *Bufo* (Laurila et al., 1997). All stimulus organisms were not fed during the experiment, but *Anax* and *Notophthalmus* were collected on 18 May—four days before testing began—from ponds

where they potentially could have fed on larval *Bufo*. In addition, *Lepomis* and *Anax* used as stimulus organisms consumed tadpoles of *Bufo* during preliminary laboratory trials conducted on 20 May, two days before testing began. However, our results argue against a role for diet in predator recognition. If the diet of a predator were important in predator recognition by *Bufo*, we would have expected to find a significant interaction between chemical stimulus and block (tadpole age). In other words, we would have expected strong reactions to *Lepomis* and *Anax* initially and a reduced response to these predators late in the experiment, when dietary cues would be less evident. We found no stimulus \times block interaction effect (Table 1) and, if anything, response to *Lepomis* and *Anax* was greater in later trials than in earlier trials (Fig. 2). Our last trials were conducted 10 days after the individuals of *Lepomis* or *Anax* used as stimulus organisms could have fed on larval *Bufo*, and it seems unlikely that dietary cues would be present in skin secretions or fecal material for this long. Thus, our results suggest that predator recognition was not mediated by dietary chemical cues. Other researchers have reached similar conclusions; dietary cues appear to play little or no role in recognition of *Anax* and other dragonfly larvae by larval *Bufo* (Anholt et al., 1996; Laurila et al., 1997; Petranka and Hayes, 1998).

Our results suggest that detection of chemical cues of potential predators and anti-predatory behavior by larval *B. americanus* is largely unaffected by larval experience. This conclusion, however, should be viewed cautiously because our laboratory-reared (naive) tadpoles had been exposed to heterospecifics chemical cues as eggs. Egg strings were present in the pond 2–3 days before we collected them, and it is possible that chemical cues from predators or damaged conspecifics may have influenced behavioral mechanisms during egg development. Sih and Moore (1993) and Moore et al. (1996) showed that eggs of the streamside salamander *Ambystoma barbouri* exposed to predator chemical cues show delayed hatching relative to

eggs not exposed to such cues. Thus, it is possible that a similar mechanism may exist in eggs of *B. americanus*. Additional studies using eggs collected from females under laboratory conditions would be needed to test this hypothesis. Although, Griffiths et al. (1998) found that Mallorcan midwife toads that had been reared in captivity for several generations and not had prior experience with predators still responded to the chemical cues of a native snake predator.

It is not surprising that recognition and avoidance of predators by tadpoles of *B. americanus* appears to be largely innate. The learning processes required to distinguish predators from non-predators is potentially fatal to larvae, and tadpoles with an innate ability to recognize predators would have a selective advantage over individuals without such a mechanism. Furthermore, because anti-predatory behavior itself is also potentially costly (Anholt et al., 1996; Griffiths et al., 1998; Lefcort, 1998), an innate response that circumvents the learning process would make it less likely that larvae mistakenly learn to perform anti-predator behavior in response to non-dangerous stimuli.

Laboratory-reared tadpoles of *B. americanus* from our study population recognized and responded to the chemical cues of two species of predators. It is not known, however, if all populations of *B. americanus* exhibit this ability, or if predator recognition without prior experience is limited to particular subpopulations. Evolutionary adaptation to local predation regimes is known to produce geographic variation in anti-predator behavior in at least some species of amphibians (e.g., Storfer and Sih, 1998).

One interesting result of our study is that toad tadpoles showed similar anti-predatory behavior in response to both *Lepomis* and *Anax* (Fig. 1) even though these predators use very different hunting styles and typically occur in different types of microhabitat (Werner and McPeck, 1994). *Lepomis* is an active hunter in open water (Holomuzki, 1995; Wellborn et al., 1996) while *Anax* uses an ambush hunting style in vegetated areas (Skelly and Werner,

1990; Wellborn et al., 1996). Our results thus suggest that predatory style does not necessarily elicit a specific anti-predatory behavior in toad tadpoles. Conversely, Lefcort (1996) found that tadpoles of *Rana utricularia* were able to differentiate between predators that use different hunting styles and performed "customized" responses.

It is also interesting that the wild-caught (experienced) tadpoles did not respond differently to the two predators (Fig. 1); tadpoles were collected from a pond that contained a large population of *Lepomis* and a very small population of *Anax*. Thus, while it is likely that the wild-caught tadpoles had close-range encounters with *Lepomis* during their development, it is likely that few had encountered *Anax*. The similar response of wild-caught tadpoles to these two predators provides further support for our conclusion that larval experience appears to play little role in the development of anti-predatory behavior in tadpoles of *B. americanus*.

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