

## Behavioral Responses of Anuran Larvae to Chemical Cues of Native and Introduced Predators in the Pacific Northwestern United States

CHRISTOPHER A. PEARL,<sup>1,2</sup> MICHAEL J. ADAMS,<sup>1</sup> GERALD S. SCHUYTEMA,<sup>3</sup> AND ALAN V. NEBEKER<sup>3</sup>

<sup>1</sup>*United States Geological Survey, Forest and Rangeland Ecosystem Science Center,  
 3200 Southwest Jefferson Way, Corvallis, Oregon 97331, USA*

<sup>3</sup>*United States Environmental Protection Agency, National Health and Environmental Effects  
 Research Laboratory, Western Ecology Division, 200 Southwest 35th Street, Corvallis, Oregon 97333, USA*

**ABSTRACT.**—We compared behavioral responses of larvae of three Pacific Northwest anurans from different hydroperiods to water borne cues of native and introduced predators. Two native anurans (Pacific Treefrog, *Pseudacris regilla*, and Northern Red-Legged Frog, *Rana aurora aurora*) and introduced Bullfrogs (*Rana catesbeiana*) responded to water conditioned by native Redside Shiners (*Richardsonius balteatus*) by increasing refuge use. The larvae of the two native anurans differed in their response to introduced predator cues. *Rana aurora aurora*, which occur in temporary and permanent waters, responded to both introduced Bluegill Sunfish (*Lepomis macrochirus*) and introduced Crayfish (*Procambarus clarkii*). *Pseudacris regilla*, which occur primarily in temporary ponds, did not respond to water borne cues from either introduced predator. The broader responses of *R. a. aurora* may indicate greater behavioral plasticity or more exposure to novel predators than experienced by *P. regilla*. Larvae of introduced *R. catesbeiana* responded strongly to cues from two fish native to the Pacific northwest but did not alter behavior in response to any of five potential predators with which they coexist in their native range. Fish that occur with *R. catesbeiana* in their native range generally find Bullfrog larvae unpalatable. This pattern suggests that Bullfrog larvae can recognize cues of novel predators that may find them palatable, which could contribute to their success as an invasive species in the region.

The ability of some amphibian larvae to respond to water borne chemical cues from predators is well documented and represents an important behavioral defense of palatable species that coexist with fish (Petranka et al., 1987; Kats et al., 1988; Lefcort, 1998). Increased refuge use and reduced activity by tadpoles are common responses to predator cues (Petranka et al., 1987; Kats et al., 1988; Lefcort and Eiger, 1993). Prey that respond to predator cues by reducing activity or seeking structural refuge are less likely to be consumed (Kats et al., 1988; Lefcort and Eiger, 1993; Skelly, 1994) but may compromise feeding, growth, and size at metamorphosis (Skelly, 1992; McCollum and Van Buskirk, 1996).

Based on extensive evidence from eastern North America, Wellborn et al. (1996) suggested that duration of ponding (hereafter, hydroperiod) and resulting variation in aquatic predators are fundamental agents shaping amphibian presence. Amphibian larvae in permanent habitats are more likely to encounter fish and large invertebrate predators than species restricted to ephemeral wetlands (Woodward, 1983; Skelly, 1996; but see Petranka and Kennedy, 1999). Behavioral responses by prey tend to be predator specific: aquatic species exhibit stronger behavioral responses to predators from within their range of the hydroperiod gradient than to predators that tend to occur in other hydroperiods (Kats et al., 1988; Wellborn et al., 1996). For example, Kats et al. (1988) tested seven palatable eastern amphibians from fishless temporary habitats and found that none responded significantly to native Green Sunfish (*Lepomis cyanellus*) predator cues. In contrast, four of five palatable species that breed in permanent wetlands increased their refuge use when exposed to green sunfish cues (Kats et al., 1988).

There have been few comparisons of antipredator behavioral responses among lowland amphibians in the western United States. Introduced predators are increasingly implicated in population declines in this region, but the ability of native species to detect and respond to novel predators is largely unknown (Hayes and Jennings, 1986; Fisher and Shaffer, 1996; Gamradt and Kats, 1996; Adams, 2000). Native anurans that are able to reduce risky behaviors in response to cues from novel predators may be better able to persist with the continued establishment of introduced predators. However, their ability to modify risky behaviors is likely a reflection of their behavioral plasticity and predator exposure over recent evolutionary time (Kats et al., 1988; Kiesecker and Blaustein, 1997).

We sought to compare predator avoidance behaviors of three Pacific Northwestern (PNW) anurans that occupy different positions along the hydroperiod gradient to native and introduced predators. Specifically, we compared refuge use by tadpoles of two native (*Rana aurora aurora* and *Pseudacris regilla*) and one introduced anuran (*Rana catesbeiana*) exposed to water borne chemical cues from native shiners (*Richardsonius balteatus*) and two introduced predators from permanent wetlands (*Procambarus clarkii* and *Lepomis macrochirus*). We also exposed *R. catesbeiana*, which have been established in the lowland PNW for up to 110 yr (Nussbaum et al., 1983), to four additional fish predators: native Northern Pike minnow (*Ptychocheilus oregonensis*), introduced Largemouth Bass (*Micropterus salmoides*), Black Crappie (*Pomoxis nigromaculatus*), and Warmouth (*Lepomis gulosus*). *Rana catesbeiana* occurs with the latter three fish, as well as *L. macrochirus* and *P. clarkii*, in portions of its native range in the eastern United States. We hypothesized that *R. catesbeiana* would demonstrate a relatively weak response to cues from predators for which unpalatability is an effective defense and with which they share habitats in their native range. We predicted that *P. regilla* would not

<sup>2</sup> Corresponding Author. E-mail: christopher\_pearl@usgs.gov

TABLE 1. Characteristics of predator and tadpole prey species used in chemical cue tests.  $N$  = Number of animals in stimulus tank. Prey characteristics are for 80 total tadpoles for each predator-prey combination except for reidside shiner  $\times$  *Rana aurora aurora*, which were for 50 tadpoles.

Predator characteristics			Prey characteristics		
Species	$N$	Wet mass (g)	Species	Wet mass (g) ( $\bar{x} \pm SE$ )	Gosner (1960) stage
Redside shiner	2	8	<i>R. a. aurora</i>	$0.38 \pm 0.10$	28–29
	4	38	<i>P. regilla</i>	$0.14 \pm 0.02$	28–29
	4	33	<i>R. catesbeiana</i>	$0.02 \pm 0.01$	25–26
Crayfish	1	32	<i>R. a. aurora</i>	$0.20 \pm 0.01$	25–26
	2	74	<i>P. regilla</i>	$0.08 \pm 0.01$	26
	2	63	<i>R. catesbeiana</i>	$0.04 \pm 0.01$	25–26
Bluegill	1	50	<i>R. a. aurora</i>	$0.16 \pm 0.02$	28–29
	1	50	<i>P. regilla</i>	$0.10 \pm 0.01$	26–27
	1	129	<i>R. catesbeiana</i>	$0.04 \pm 0.01$	25–26
<i>N. pikeminnow</i>	2	22	<i>R. catesbeiana</i>	$0.05 \pm 0.01$	25–26
Largemouth bass	3	55	<i>R. catesbeiana</i>	$0.08 \pm 0.01$	25–26
Warmouth	2	67	<i>R. catesbeiana</i>	$0.04 \pm 0.01$	25–26
Black crappie	1	62	<i>R. catesbeiana</i>	$0.06 \pm 0.01$	25–26

respond to cues of introduced predators associated with permanent ponds. We predicted that *R. a. aurora*, which are palatable to most predators and occupy wetlands of temporary and permanent hydroperiods, should be more plastic behaviorally than the other two species and would respond to cues of all three predators by increasing use of refuges.

#### MATERIALS AND METHODS

*Test Organisms.*—All species tested occur in the Willamette Valley, Oregon. Tadpoles of native *R. a. aurora* and introduced *R. catesbeiana* were raised from eggs collected from permanent ponds near Eugene, Oregon, and *P. regilla* were raised from eggs collected from a temporary wetland near Corvallis, Oregon. We collected Redside Shiner, Bluegill, Northern Pikeminnow, Warmouth, Largemouth Bass, and Black Crappie from the Willamette River near Corvallis, and crayfish from a permanent pond near Eugene. Test animals were housed in 38-liter glass aquaria with flowing well water for at least two weeks before experiments. Tadpoles were provided rabbit food pellets ad libitum prior to tests. Crayfish were fed carrots and annelid worms (*Lumbriculus variegatus*). Fish were fed earthworms (*Lumbriculus terrestris*) and mealworms (*Tenebrio molitor*). Predators were not fed for 18 to 24 h preceding a test and were never fed amphibians. Tadpole developmental stage (Gosner, 1960) was standardized within and among species, but predator size varied with availability (Table 1).

*Test Procedures.*—Water used in experimental trials was obtained from groundwater wells near the Willamette River at Corvallis, Oregon. Mean ( $\pm$  SE) water quality parameters were similar to conditions in Willamette Valley wetlands: hardness,  $38.9 \pm 2.8$  mg/L as  $\text{CaCO}_3$  ( $N = 30$ ); alkalinity,  $39.2 \pm 3.6$  mg/L as  $\text{CaCO}_3$  ( $N = 19$ ); conductivity,  $111.1 \pm 6.6$   $\mu\text{S}/\text{cm}$  ( $N = 34$ ); and median pH (measured by electrode) was 6.6 ( $N = 16$ ).

The test apparatus was similar to System B of Petranka et al. (1987) and consisted of three pairs of polyethylene tanks ( $35 \times 23 \times 22$  cm) and a waste catchment. Each series was arranged at three heights in

a linear sequence and filled to a depth of 12.5 cm with 10 liters of well water. The water flowed sequentially through tygon tubing at 0.5 L/min from the uppermost tanks through intermediate stimulus tanks containing predators into the refuge tanks containing prey through 6 mm ID tubing. The outlet half of each refuge tank contained an opaque plastic plate ( $17.5 \times 23$  cm) supported by neoprene stoppers 2.5 cm from the bottom. Water exited the refuge tanks and flowed into a waste catchment. At the start of an experiment, all of the tanks on the right-hand side of the apparatus were designated as test tanks, and those on the left-hand side as controls. These designations were reversed after each of the eight replicate exposures per chemical-cue trial. All tanks were vigorously rinsed and brushed four times (two times with tap water, once with distilled water, and once with well water) before the next replicate was conducted. Tygon tubing was also rinsed four times between trials.

We conducted eight tests for each combination of prey and predator species, except the *R. a. aurora*  $\times$  reidside shiner tests, in which one shiner escaped and the experiment was terminated after five tests (Table 2). Each test included 10 observations of tadpole position. At the start of a test, a predator species (e.g., one bluegill, one or two crayfish, two or four reidside shiners) was placed in one of the stimulus tanks. The control stimulus tank contained only water. After 30 min, small plugs were removed from the tubing drains of the reservoir tanks. Concurrently, five prey tadpoles were added to test and control refuge tanks. Groups rather than individual tadpoles were used to account for social interactions that might influence responses under natural conditions (Petranka et al., 1987). Beginning 10 min after introduction of tadpoles, we recorded the numbers of tadpoles outside of the plate refuge at 1-min intervals for 10 min. Observations were made through a small opening (approximately  $15 \times 8$  cm) in an opaque white plastic curtain to minimize disturbance of test animals. The same predator individuals were used throughout the eight tests for each predator-prey combination, but tadpoles were replaced prior to each replicate exposure. No tadpoles were reused.

TABLE 2. Response of *Rana aurora aurora*, *Pseudacris regilla*, and *Rana catesbeiana* tadpoles to water conditioned by crayfish or fish. Origin (N)ative to Pacific Northwestern United States, (I)ntroduced to PNW from eastern United States. *N* = Number of replicate trials. *P*-value for difference between control and test trials: \* = significant at Bonferroni-adjusted rejection criteria (see Materials and Methods, Analysis), <sup>NS</sup> = not significant at adjusted rejection criteria.

Prey	Predator	Origin	N	Mean proportion of prey outside of refuge		P
				Test (SE)	Control (SE)	
<i>R. a. aurora</i>	Redside Shiner	N	5	0.62 (0.09)	0.89 (0.05)	0.015*
	Crayfish	I	8	0.64 (0.03)	0.72 (0.03)	0.023*
	Bluegill	I	8	0.70 (0.04)	0.83 (0.03)	0.017*
<i>P. regilla</i>	Redside Shiner	N	8	0.65 (0.04)	0.89 (0.05)	0.001*
	Crayfish	I	8	0.78 (0.08)	0.81 (0.05)	0.397 <sup>NS</sup>
	Bluegill	I	8	0.79 (0.05)	0.87 (0.04)	0.165 <sup>NS</sup>
<i>R. catesbeiana</i>	Redside Shiner	N	8	0.70 (0.05)	0.88 (0.04)	0.004*
	N. Pikeminnow	N	8	0.53 (0.04)	0.73 (0.03)	0.001*
	Crayfish	I	8	0.85 (0.03)	0.86 (0.04)	0.349 <sup>NS</sup>
	Bluegill	I	8	0.66 (0.08)	0.74 (0.08)	0.364 <sup>NS</sup>
	Warmouth	I	8	0.71 (0.05)	0.89 (0.03)	0.023 <sup>NS</sup>
	Black Crappie	I	8	0.67 (0.06)	0.75 (0.05)	0.174 <sup>NS</sup>
	Largemouth Bass	I	8	0.80 (0.05)	0.85 (0.04)	0.258 <sup>NS</sup>

To assess palatability, we placed prey tadpoles ( $N = 5-12$  of the same Gosner stages as those tested) together with one Bluegill or two Redside Shiners in a separate polyethylene tank ( $35 \times 23 \times 22$  cm) not used in our experiments. This procedure was repeated for all three anuran species with a Bluegill predator, and for two of three anurans (*P. regilla* and *R. catesbeiana*) with redside shiners. After 24 h, we recorded the number of tadpoles remaining.

**Analysis.**—The response variable in the cue experiment was the average proportion of tadpoles outside the refuge during the 10-min trial. Proportions were normalized with an angular transformation prior to data analysis. Normality of transformed data was confirmed with Kolmogorov-Smirnov tests for each comparison (SigmaStat 2.0; Jandel Corporation, San Rafael, California). Extensive experimentation of anuran behavioral responses has demonstrated a unidirectional response (prey species that detect cues increase, rather than decrease, cover use; see Kats et al., 1988), so differences between test and control means were examined with a one-tailed *t*-test (SigmaStat 2.0; Jandel Corporation, San Rafael, California). We used a sequential Bonferroni adjustment to accommodate multiple comparisons for each prey species (Rice, 1989). Rejection criteria were adjusted for three comparisons for *R. a. aurora* and *P. regilla* tests, and for seven comparisons for the Bullfrog tests. For example, the lowest *P*-value for *R. a. aurora* was compared with an  $\alpha' = 0.017$  ( $\alpha' = 0.05/3$  comparisons); if that was significant, the second lowest *P*-value was compared with  $\alpha' = 0.025$  ( $\alpha' = 0.05/2$ ), etc.

## RESULTS

All three anurans demonstrated significantly higher refuge use in response to water conditioned by at least one of the predators tested (Table 2). *Pseudacris regilla* larvae responded to cues of native Redside Shiners and did not respond to chemical cues of either introduced predator. *Rana a. aurora* larvae increased refuge use in

response to cues from all three predators. Introduced *R. catesbeiana* larvae responded significantly to cues from both northwestern native fish (Northern Pikeminnow and Redside Shiner) but did not respond to cues from any of the fish with which they share their native range.

In the palatability trials, Bluegill consumed 100% of available *R. a. aurora* and *P. regilla* larvae, and 0% of *R. catesbeiana* larvae offered. Redside Shiners consumed 100% of *P. regilla* and *R. catesbeiana* larvae offered.

## DISCUSSION

This experiment offers the first comparison of refuge-use behavior in response to chemical cues from native and introduced predators for lowland PNW anurans. These findings address the capacity for selected native amphibians to reduce their predation risk in the presence of different introduced predators. All three anuran species responded to water conditioned with native redside shiners, suggesting that shiners may be effective predators that coexist often enough with the tested anurans to elicit avoidance behaviors. Our feeding trials showed that redside shiners readily consume small numbers of *P. regilla* and *R. catesbeiana* tadpoles in laboratory tanks. Despite their use of different portions of the wetland hydroperiod gradient for breeding sites, all three anurans may be exposed to predation pressure by shiners. Redside Shiners occupy a variety of aquatic habitats from lakes to moderately fast streams and large rivers in lower elevations of the Willamette Basin (Scott and Crossman, 1973; Altman et al., 1997). They can move upstream into intermittent drainages during spring high water or reach ponds as a result of river flooding (Lindsey and Northcote, 1963).

Differential responses to introduced predator cues probably reflect some combination of behavioral plasticity of prey species and selective forces imposed by the predator. Kiesecker and Blaustein (1997) found that larvae of *R. a. aurora* sympatric with introduced *R. catesbeiana* were better able to sense chemical cues of *R. catesbeiana* and were less susceptible to Bullfrog

predation than allopatric larvae. They inferred that *R. catesbeiana* exert selective pressure on predator detection of *R. a. aurora* and refuge use and that such behaviors may be favored over relatively short time periods (approximately 50 yr). We did not test palatability of tadpoles of *R. a. aurora*, but other studies have demonstrated their palatability to most predators, including introduced centrarchid fishes (*Micropterus dolomieu*; Kiesecker and Blaustein, 1998), Roughskinned Newts (*Taricha granulosa*; Wilson and Lefcort, 1993), and adult *R. catesbeiana* (Kiesecker and Blaustein, 1997). That *R. a. aurora* tadpoles responded to both native and introduced predators in our study may indicate a well-developed ability to respond to predators from across the hydroperiod gradient. Such a plastic response, along with early breeding, may partially explain the ability of *R. a. aurora* to breed successfully in a broad range of hydroperiods.

In contrast, palatable larvae of *P. regilla* modified their behavior when exposed to cues of a native predator but did not respond to either introduced species, suggesting that the test population can respond to predators but that the introduced species have not exerted sufficient selective pressure for *P. regilla* to develop a response. In the Willamette Valley, *P. regilla* often breed in isolated temporary pools that dry by early summer, and tadpoles are thought to demonstrate high activity rates and rapid growth to achieve metamorphosis prior to desiccation (Nussbaum et al., 1983). The response of *P. regilla* to Redside Shiners in this experiment and their avoidance of injured conspecifics in the field (Adams and Claeson, 1998) suggest this species possesses elements of both the high activity-rapid growth strategy and a predator-avoidance strategy, although not to the extent demonstrated by *R. a. aurora*. Both introduced crayfish and Bluegill occur in the Willamette Valley in permanent waters but probably only rarely access larvae of *P. regilla* in temporary habitats. That none of the three tested amphibians responded significantly to crayfish is consistent with other work suggesting their lower efficiency as predators on anuran larvae (Lefcort, 1996).

*Rana catesbeiana* generally require permanent waters to complete larval development, and their relative unpalatability affords larvae some defense against fish predators (Kruse and Francis, 1977; Woodward, 1983). Unpalatability has been linked to lack of behavioral modifications in larvae of several bufonids. For example, Laurila et al. (1997) suggested that unpalatability of Common Toads (*Bufo bufo*) accounted for their lack of response to chemical cues of a sympatric odonate predator. Kiesecker et al. (1996) found that larvae of *Bufo boreas* modified behavior in response to three predators that find them palatable (two insects and one snake) but did not respond to cues of two predators that find them unpalatable (one newt and one fish). Larvae of *Bufo terrestris* are distasteful to Warmouth and reduce their activity but do not increase refuge use when exposed to water conditioned by this predator (Lefcort, 1998).

Experimental evidence on behavioral responses of *R. catesbeiana* to predator cues is mixed. Larvae of *R. catesbeiana* larvae from their introduced range were significantly less active when exposed to water conditioned by Roughskinned Newts, which consumed

larvae of *R. catesbeiana* in lab settings (Lefcort and Eiger, 1993). Larvae of *R. catesbeiana* from their native range reduced activity more in response to dragonfly larvae than in response to native mudminnows, which find *R. catesbeiana* less palatable than dragonflies (Relyea, 2001). Kats et al. (1988) found that larvae of *R. catesbeiana* from their native range increased refuge use when exposed to chemical cues from Green Sunfish. In that study, no adjustment for multiple comparisons was made; thus, it remains unclear whether this response was significant. In our study, larvae of *R. catesbeiana* increased refuge use in response to cues of two fish predators native to our study area (Redside Shiner and Northern Pikeminnow) and did not respond significantly to the five predators tested with which they are sympatric in their native range.

Our results raise the possibility that larvae of *R. catesbeiana* can discriminate between "familiar" predators from their native range (against which their unpalatability provides some defense) and predators with which they have not shared a native range and which may either find them more palatable or may not have evolved to avoid them. Both Roughskinned Newts (Lefcort and Eiger, 1993) and Redside Shiners (this study) consume small *R. catesbeiana* in lab aquaria where alternate prey are not provided. They appear to be avoided by Bluegill and Largemouth Bass when these predators are provided more palatable options (Kruse and Francis, 1977; Werner and McPeck, 1994). Redside Shiners, Northern Pikeminnow, and Roughskinned Newts may represent significant predators of *R. catesbeiana* in portions of its introduced range, and larval unpalatability may be a lesser deterrent with these novel predators than with predators in its native range. Testing of additional populations of *R. catesbeiana* is needed, but a sophisticated ability to modify behavior only in response to more dangerous novel predators could contribute to their success as an invasive species (e.g., Hazlett, 2000).

Our results suggest the three tested anuran larvae are able to differentiate between predator cues and may alter refuge use as a function of both exposure history and palatability. Many introduced predators, particularly game fish, are implicated in population declines of western anurans, and interactions are likely focused on larval stages (Hayes and Jennings, 1986; Gamradt and Kats, 1996; Kiesecker and Blaustein, 1998; Adams 2000). Continued loss of temporary wetlands and construction of permanent ponds in the western United States (Kentula et al., 1992; Bernert et al., 1999) may increase juxtaposition of pond breeding amphibians with introduced predators that require permanent hydroperiods. Additional inquiry into these behavioral modifications is needed to elucidate their importance in predicting coexistence and persistence of native amphibians and introduced predators in western wetlands.

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