



RESEARCH PAPER

Antipredator Behavior of American Bullfrogs (*Lithobates catesbeianus*) in a Novel Environment

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Abstract

Invasive species capable of recognizing potential predators may have increased establishment rates in novel environments. Individuals may retain historical predator recognition and invoke innate responses in the presence of taxonomically or ecologically similar predators, generalize antipredator responses, or learn to avoid risky species in novel environments. Invasive amphibians in aquatic environments often use chemical cues to assess predation risk and learn to avoid novel predators via direct experience and/or associated chemical cues. Ontogeny may also influence recognition; experience with predators may need to occur at certain developmental stages for individuals to respond correctly. We tested predator recognition in invasive American bullfrog (*Lithobates catesbeianus*) tadpoles that varied in experience with fish predators at the population and individual scale. We found that bullfrog tadpoles responded to a historical predator, largemouth bass (*Micropterus salmoides*), only if the population was locally sympatric with largemouth bass. Individuals from a population that did not co-occur with largemouth bass did not increase refuge use in response to either largemouth bass chemical cues alone or chemical cues with diet cues (largemouth bass fed bullfrog tadpoles). To test whether this behavioral response was generalized across fish predators, we exposed tadpoles to rainbow trout (*Oncorhynchus mykiss*) and found that tadpoles could not recognize this novel predator regardless of co-occurrence with other fish species. These results suggest that environment may be more important for predator recognition than evolutionary history for this invasive species, and individuals do not retain predator recognition or generalize across fish predators.

Introduction

Avoiding predation in complex systems requires prey species to correctly recognize and respond to predation risk. Assessing predatory risk is important in accurately informing trade-off decisions regarding foraging, mating, and other behaviors that could potentially increase exposure to predatory threats (Lima & Dill 1989). When biological invasions occur, novel predator/prey interactions can significantly impact population dynamics of native and non-native species within a community (Payne et al. 2004). Recognizing novel predators may therefore necessitate a combination of behavioral influences; in addition to an organism's

evolutionary history and innate responses, local environment and individual learning may allow invading organisms to successfully reduce predation risk (Epp & Gabor 2008; Ferrari et al. 2009).

Novel environments present a particular challenge to invading populations in part because predators have unfamiliar chemical, physical, and behavioral signatures that may reduce a species' ability to perceive risk (Paoletti et al. 2011). Perception of novel predators by invaders may be influenced by evolutionary history or taxonomic relatedness to predators from their native region, which may allow individuals to respond appropriately to risk (Multipredator Hypothesis; Blumstein 2006). Alternatively, a general

sensitivity to novel stimuli can result in appropriate antipredator behaviors (generalization hypothesis, Ferrari et al. 2008). Recognition of novel predators can also be a learned response. For example, many aquatic species can learn to recognize predators via direct contact or through the pairing of species-specific chemical cues with predator diet cues produced by the consumption of conspecific prey (Mathis & Smith 1993). The intensity of antipredator responses can also match the species-specific risk associated with different predators, with individuals learning to gauge response intensity by assessing predator and alarm cue concentrations (threat-sensitive predator avoidance, Helfman 1989; Ferrari & Chivers 2006).

Innate and learned antipredator behaviors need not be mutually exclusive (Epp & Gabor 2008; Gonzalo et al. 2009). However, we posit that invasive populations undergo significant pressure to recognize novel predators (i.e., threat-sensitive predator avoidance) and thus recognition would favor immediate predation threats over evolutionary history. As such, individual experience with local predator communities may weigh more heavily relative to historical predators (Gherardi et al. 2011). Invasive species may therefore not be capable of recognizing historical predators from their native range. If exposed to historical predators, individuals from an invasive population may not respond with appropriate antipredator behaviors unless antipredator behaviors are generalized across taxonomically or ecologically similar species (i.e., multipredator hypothesis). Further, the ontogenetic timing of exposure to a predator can influence the ability of prey to respond appropriately. For example, wood frogs (*Rana sylvatica*) exposed to predatory tiger salamander (*Ambystoma tigrinum*) chemical cues during the embryo stage responded appropriately when exposed to this same predator as a tadpole. Wood frog tadpoles that were not pre-exposed as embryos, however, were unable to learn how to recognize tiger salamanders over ontogeny (Ferrari & Chivers 2009a). The timing of predator exposure, in both an evolutionary and ontogenetic context, can influence how an individual responds to both known and unknown predators.

Amphibians in particular are highly sensitive to predator chemical cues and can respond strongly to associated predator diet cues (Chivers & Mirza 2001). Larval amphibians may respond to predator chemical cues with increased refuge use, decreased activity rates, and cryptic color change (Petranka et al. 1987; Kats et al. 1988; Garcia et al. 2004). Behaviors that require individuals to hide or reduce activity rates,

however, incur a cost owing to consequent decreases in feeding, growth, and development rates (Lima & Dill 1989; Skelly 1992; Teplitsky et al. 2003). For larval amphibians in novel environments, trade-offs between avoiding predators and maintaining a developmental trajectory can be particularly complex. Correctly assessing risk will benefit non-native tadpoles via increased foraging, growth, and survival rates relative to tadpoles that incorrectly allocate time to antipredator vigilance. Conversely, biological resistance to invasion can be enhanced if non-native tadpoles are incapable of recognizing the chemical cues of novel predators.

Biologically invaded communities can be model systems in which to test recognition of novel predators. To isolate the genetic vs. environmental influences on predator recognition, we manipulated predator exposure in an invasive amphibian species across populations and over ontogeny. The American bullfrog (*Lithobates catesbeianus*) has successfully invaded freshwater habitats around the world and is highly successful in lentic freshwater environments throughout the northwestern United States (Hayes & Jennings 1986; Funk et al. 2010). Bullfrogs have significantly altered aquatic community dynamics via novel interspecific interactions (Kiesecker & Blaustein 1997, 1998; Pearl et al. 2004). Several studies have shown that bullfrogs can respond to predator chemical cues from sympatric species (Pearl et al. 2003; Smith et al. 2008a) and do not respond to chemical cues from allopatric predator species (Smith et al. 2008b), but manipulation of individual experience has not previously been carried out.

We tested the hypothesis that invasive American bullfrog tadpoles would vary in their response to predatory fish as a function of experience. Further, we tested whether an antipredator response was generalized across fish species. We used two populations of bullfrogs, one from a pond with predatory fish (sympatric) and another from a pond with no predatory fish (allopatric). We manipulated individual exposure to fish predators using individuals collected in the egg stage (laboratory-reared) and tadpole stage (wild-caught). Individuals therefore varied in evolutionary and ontogenetic timing of exposure to predator chemical cues from largemouth bass (*Micropterus salmoides*), a historical predator of bullfrogs in their native range and an exotic game species common in the northwestern United States, and rainbow trout (*Oncorhynchus mykiss*), a predatory species native to the northwestern United States.

Diet and feeding strategies of these two predatory fish species are similar across multiple habitats,

particularly in Oregon where competition in sympatric populations is more common because of pond stocking for recreational fisheries (Shrader & Moody 1997). Both species are generalist, opportunistic feeders that feed on macroinvertebrates and aquatic vertebrate prey (e.g., fishes, crustaceans, and amphibians) during the adult stages (Carmichael 1983; Hodgson et al. 1991; Hodgson & Hansen 2005). The manipulation of individual experience with both fish predators allowed us to determine whether bullfrog tadpoles were capable of recognizing a predatory threat they had never encountered, had never encountered but historically coexisted with, or had encountered at various points over ontogeny. Further, we used multiple types of chemical cues to quantify the influence of species-specific chemical cues compared to diet cues (Laurila et al. 1997). We also verified palatability of bullfrog tadpoles with both largemouth bass and rainbow trout (Kruse & Francis 1977).

Methods

Bullfrog Egg Collection

Bullfrog egg masses were collected from two permanent privately owned ponds in the Willamette Valley, Oregon, on June 22, 2011, and June 30, 2011. In the absence of a thorough record of gene flow between Oregon bullfrog populations (Funk et al. 2010), we selected sites with a low likelihood of interspersions. Bullfrog dispersal between these two ponds, which are separated by a distance of 17.5 km, is highly improbable as bullfrogs exhibit strong site fidelity. Further, bullfrog movement in this agricultural landscape is strongly limited by fragmentation except when barriers are temporarily overridden by flooding events (Gahl et al. 2009). Thus, one of our sites (site 1) is located outside the flood plain to limit the potential of flood-driven dispersal of both bullfrogs and fish. Three egg masses were collected from site 1, which contains no fish species and is located at 44°49'16.42" N and 123°11'55.57" W at 61 m elevation. Another three egg masses were collected from site 2, which contains largemouth bass and is located at 44°54'23.40" N and 123°11'06.42" W at 55 m elevation. All egg masses were transported to Oregon State University and held in an environmental chamber with constant temperature (26°C) and controlled photoperiod (14L: 10D). Egg masses were held in 30-l HDPE plastic tubs with filtered, dechlorinated tap water. Tadpoles were transferred to clutch-specific 30-l tubs within 1 d of hatching and reared until Gosner (1960) stage 25.

Bullfrog Tadpole Collection

Stage 25 tadpoles (Gosner 1960) from both site 1 and site 2 were collected no more than 7 days prior to each experimental trial. Tadpoles used in the largemouth bass experiment were collected on Sept. 7, 2011, from site 1 and Sept. 8, 2011, from site 2. Tadpoles used in the rainbow trout experiment were collected from both sites on Sept. 28, 2011. All tadpoles were transported to Oregon State University. Wild-caught and laboratory-reared tadpoles were all kept at low densities (8 hatchlings/l; 1 stage 25 tadpole/l) and fed *ad libitum* algal pellets and a 3:1 ratio of ground rabbit chow and fish flakes.

Predatory Fish Survey, Collection, and Cue Preparation

Sites were extensively sampled on multiple occasions using minnow traps, seine, hoop, and dip nets to assess the fish community and inform selection of experimental predator species; sites were also selected based on landowner consent and historical knowledge of the flood regime. Five largemouth bass adults were collected 4 d prior to the experimental trial from the Willamette River near Newburg, Oregon. Fish were held in two 385-l cattle tanks filled with 250 l of dechlorinated, filtered tap water in an Oregon State University environmental chamber with constant temperature (20°C) and controlled photoperiod (14L: 10D). Two days prior to the experiment, half the water was removed from both cattle tanks and replaced with dechlorinated, filtered tap water to maintain water quality. No further water additions or removals were performed prior to the experiment.

To create two types of largemouth bass chemical cue treatments, one group (two individuals, body lengths = 37 and 41 cm) was fed earthworms and crickets *ad libitum*, while the other group (three individuals, average body length = 24.6 ± 1.2 cm) was fed bullfrog tadpoles *ad libitum* from the laboratory-reared site 1 and site 2 groups. On average, largemouth bass consumed three bullfrog tadpoles/d of captivity. Sixteen rainbow trout (average body length = 16.2 ± 0.4 cm) were obtained from Oregon State University's Fish Research Laboratory and were held in two 200-l tanks filled with filtered well water 2 days prior to the experiment. No water additions or removals were performed after this point. One group was fed fish flakes, and the other was fed bullfrog tadpoles (3 bullfrog tadpoles/fish/d from the site 1 and site 2 populations). The rainbow trout used were from brood year Nov. 2009.

Palatability Trials

Both largemouth bass and rainbow trout were fed bullfrog tadpoles to assess palatability. Three largemouth bass individuals (average body length = 10.3 ± 0.8 cm) were collected from site 2 and transported to Oregon State University. All three individuals were held for 24 h in a 385-l tank filled with dechlorinated, filtered tap water and then fed 3 bullfrog tadpoles (Gosner stage 25) per fish. Largemouth bass were observed consuming bullfrog tadpoles, and no tadpoles remained in the tank after 1 h. Eight rainbow trout (average body length = 14.8 ± 0.9 cm) were collected from the Oregon State University Fish Research Laboratory and held in a 200-l tank. Three bullfrog tadpoles (Gosner stage 25) per fish were added to the tank, and no tadpoles remained after a period of 6 h. All fish were observed for an additional 12 h to ensure no deleterious effects occurred as a result of bullfrog tadpole consumption.

Refuge-Use Experimental Design: Bullfrog/Largemouth Bass Experiment

We quantified refuge use in bullfrog tadpoles that varied in experience with largemouth bass at the population and individual scale on Sept. 15, 2011. In a fully factorial 3 × 4 design, bullfrog tadpoles were exposed to three predator chemical cue treatments: (1) largemouth bass chemical cues, (2) largemouth bass chemical and diet cues, and (3) a control treatment. Bullfrog experience treatments included (1) laboratory-reared tadpoles from a fishless population (allopatric laboratory-reared), (2) laboratory-reared tadpoles from a largemouth bass pond (sympatric laboratory-reared), (3) wild-caught tadpoles from a fishless population (allopatric wild-caught), and (4) wild-caught tadpoles from a largemouth bass pond (sympatric wild-caught). All treatment combinations were replicated six times for a total of 72 experimental units. Size differences

between the four tadpole groups were not statistically different (Table 1).

Experimental units (19 cm × 32 cm clear plastic tubs) contained one refuge consisting of an 8 cm × 6 cm piece of corrugated black plastic. Placement of the refuge rotated clockwise around the four corners of the unit across all 72 units. All units contained 1 l of control water (filtered and dechlorinated tap water) and 1 l of the randomly assigned predator chemical cue treatment. Individual tadpoles were randomly selected from each group, added to units, and given a 30-min acclimation period before behavioral observations began. Behavioral spot-checks and recording of refuge use were conducted every 20 min for a total of 10 observations per unit beginning at 11:00 h. The proportion of time spent in refuge across all 10 observations was calculated for all individuals. Observers were blind to assigned treatment combinations, and all experimental units were located behind observation blinds to limit observer disturbance. Hypotheses were tested using one-way ANOVA, and pairwise comparisons were tested using a Tukey’s test in SYSTAT 11.1 (Chicago, IL, USA).

Refuge-Use Experimental Design: Bullfrog/Rainbow Trout Experiment

The bullfrog/rainbow trout experimental trial occurred on Sept. 30, 2011. We tested whether increased refuge use in experienced bullfrog tadpoles was a generalized predator response or predator specific by exposing bullfrogs to a novel predator native to the northwestern United States. Using the same replicated, fully factorial design and experimental protocol as the bullfrog/largemouth bass experiment, four tadpole groups that varied in experience with predatory fish were exposed to three chemical cue treatments. Size differences between the four tadpole groups were not statistically different (Table 1). Hypotheses and pairwise comparisons were tested using Friedman’s nonparametric test in SYSTAT 11.1.

Table 1: Mean size data with standard errors for all four American bullfrog (*Lithobates catesbeianus*) tadpole groups for the largemouth bass (*Micropterus salmoides*) chemical cue exposure experiment and the rainbow trout (*Oncorhynchus mykiss*) chemical cue exposure experiment. Neither snout/vent length nor mass was significantly different between the four groups for either experiment

	Allopatric laboratory-reared	Sympatric laboratory-reared	Allopatric wild-caught	Sympatric wild-caught
Bullfrog/largemouth bass experiment				
Snout/vent length (mm)	14.23 (±0.26)	13.97 (±0.39)	12.17 (±0.20)	13.82 (±0.28)
Mass (mg)	54.74 (±2.85)	54.91 (±4.43)	30.46 (±1.39)	41.5 (±2.21)
Bullfrog/rainbow trout experiment				
Snout/vent length (mm)	14.05 (±0.49)	14.33 (±0.38)	13.57 (±0.39)	13.92 (±0.46)
Mass (mg)	55.04 (±5.03)	51.96 (±3.02)	46.73 (±3.23)	51.71 (±4.53)

Results

Bullfrog/Largemouth Bass Experiment

We found that allopatric and sympatric bullfrog populations differed significantly in refuge use ($p = 0.013$, Table 2, Fig. 1) and largemouth bass chemical cue treatments had a significant effect on individual refuge-use behavior ($p = 0.007$; Table 2). A pairwise comparison of treatment groups revealed that the sympatric laboratory-reared group exposed to both chemical cue types differed significantly from control

Table 2: Results of an ANOVA on effects of largemouth bass (*Micropterus salmoides*) predation risk and individual experience with fish predators on American bullfrog (*Lithobates catesbeianus*) tadpole refuge use

Response variable	Effect	SS	df	F	p
Refuge use	CC	0.41	2	5.32	0.007*
	Group	0.45	3	3.90	0.013*
	CC × Group	0.37	6	1.60	0.164
	Error	2.29	60		

CC is the effect of chemical cues, and group indicates the four different tadpole groups. df, degrees of freedom, asterisks indicate significance.

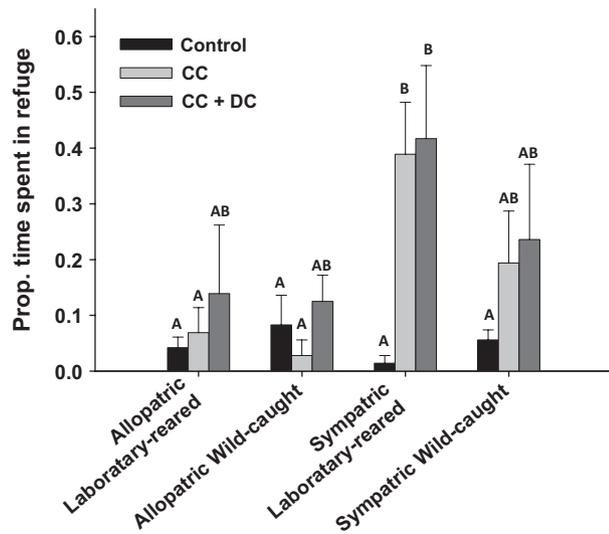


Fig. 1: Proportion of time spent in refuge by American bullfrog tadpoles (*Lithobates catesbeianus*) during exposure to largemouth bass chemical cues (CC) and largemouth bass (*Micropterus salmoides*) chemical cues plus diet cues from consumed bullfrog tadpoles (CC + DC) treatments. Allopatric laboratory-reared and wild-caught groups indicate individuals collected at the egg and tadpole stage, respectively, from a pond containing no predatory fish. Sympatric laboratory-reared and wild-caught groups indicate individuals collected at those respective stages from a pond with predatory largemouth Bass. A significant chemical cue effect and group were found ($p = 0.007$ and $p = 0.013$, respectively). Significant pairwise comparisons ($p < 0.015$) are designated with different letters (A, B).

treatments and the majority of the allopatric treatment groups (Fig. 1).

Bullfrog/Rainbow Trout Experiment

Individual bullfrog tadpoles from both the sympatric and allopatric populations did not respond to either type of rainbow trout chemical cue with a significant increase in refuge use (Friedman’s test, $X_{3,4} = 6$, $p = 0.1$). We found no significant pairwise comparisons using the significance threshold of $\alpha = 0.0167$ to account for multiple comparisons (Fig. 2). We did, however, find a non-significant trend ($p = 0.080$), between the sympatric laboratory-reared group and other treatment groups exposed to chemical cues with diet cues; these tadpoles differed from other treatment groups by responding to rainbow trout chemical cues and diet cues with an increase in refuge use (Fig. 2). One outlier was removed from the analysis in the allopatric laboratory-reared group.

Discussion

We found that individuals from a bullfrog population that is sympatric with largemouth bass were able to respond to largemouth bass chemical cue with

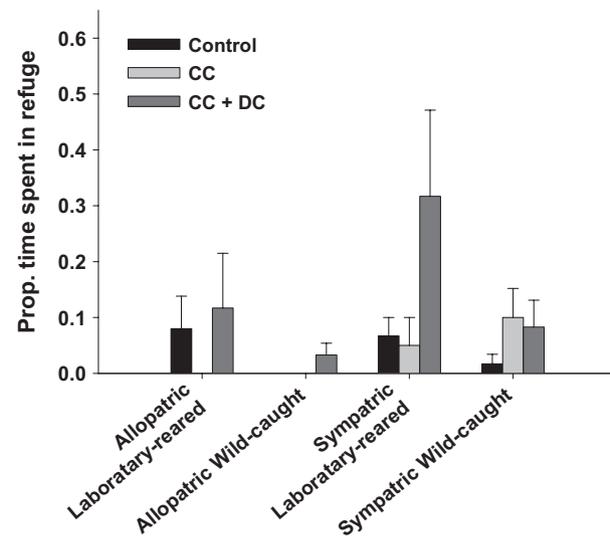


Fig. 2: Proportion of time spent in refuge by American bullfrog tadpoles (*Lithobates catesbeianus*) during exposure to rainbow trout (*Oncorhynchus mykiss*) chemical cues (CC) and rainbow trout chemical cues plus diet cues from consumed bullfrog tadpoles (CC + DC) treatments. Allopatric laboratory-reared and wild-caught groups indicate individuals collected at the egg and tadpole stage, respectively, from a pond containing no predatory fish. Sympatric laboratory-reared and wild-caught groups indicate individuals collected at those respective stages from a pond with predatory fish, but not rainbow trout.

increased refuge use. Individuals collected from a pond that contained no predatory fish (allopatric bullfrogs) did not recognize largemouth bass as a threat and thus did not respond with increased refuge use. These results suggest that local environment may have a stronger influence on predator recognition and response than evolutionary history in invasive bullfrog populations in Oregon. Largemouth bass, a species that co-occurs with bullfrogs throughout much of their native range (Fig. 3), are a historical predator for bullfrogs, and studies have determined that bullfrogs can respond to largemouth bass chemical cues with altered microhabitat use (Pearl et al. 2003; Smith et al. 2008a). Regardless of this historic overlap, bullfrogs occupying a fishless pond in Oregon were not able to recognize this ancestral predator.

The multipredator hypothesis posits that antipredator behaviors are rapidly lost in a predator-free environment (Blumstein 2006). Individuals are, however, predicted to display appropriate responses during their first encounter with a historical predator provided they have experienced at least one predator species in their lifetime. This hypothesis suggests that linkages between an antipredator behavior and benefits of exhibiting that behavior during non-predatory situations are what allow these behaviors to be maintained even when predators have been removed. Our study did not support this hypothesis as individuals from a population without largemouth bass were unable to

recognize cues from this historical predator. One caveat to this hypothesis is that the relative costs of maintaining predator recognition will influence the likelihood of persistence. Behavioral modifications such as increasing refuge use and suspending key activities such as foraging may significantly reduce individual fitness. Therefore, the selective pressure to eliminate this costly behavior may have outweighed any pleiotropic benefits. Further, exposure to taxonomically similar predators at some point in an individual's life is more likely to elicit an antipredator response to historical predators, and the allopatric bullfrogs in our study do not co-occur with predatory fish. This population was likely only exposed to macroinvertebrate predators, and thus, recognition of a historical fish predator may not have been possible.

To address the question of whether bullfrog tadpoles exhibit a generalized response to novel predators, we exposed bullfrog tadpoles to a second fish predator, rainbow trout. This species is native to the northwestern United States, and bullfrog populations in the Willamette Valley, Oregon, could potentially encounter this fish predator after a large flooding event, through stocking, or when dispersing to other aquatic habitats. We found that neither the largemouth bass sympatric tadpoles nor the largemouth bass allopatric tadpoles responded to rainbow trout chemical cues with increased refuge use. This inability to respond appropriately to a novel predator suggests

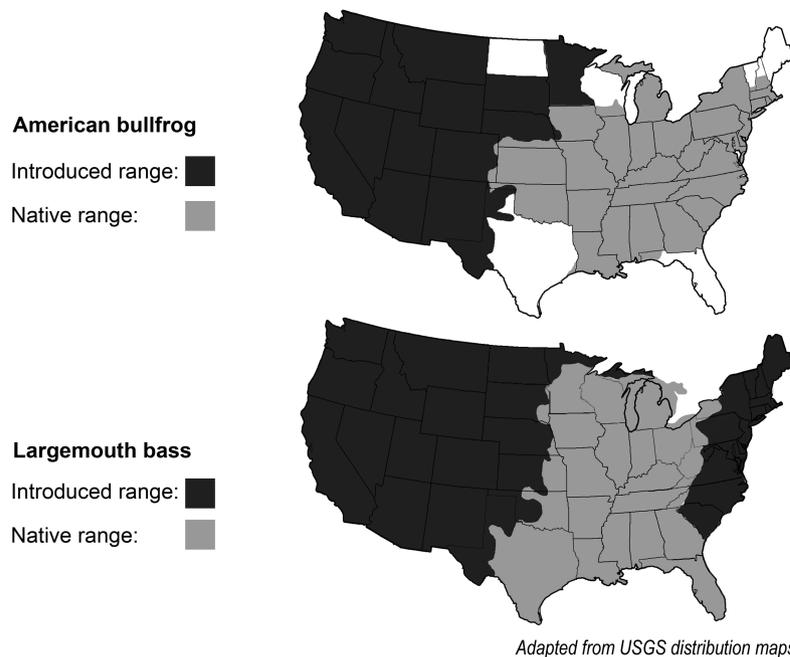


Fig. 3: Map showing the overlap of the (A) introduced and (B) native species ranges within the continental United States for both American bullfrogs (*Lithobates catesbeianus*) and largemouth bass (*Micropterus salmoides*). Data were adapted from USGS distribution maps for both species.

individuals either had no evolutionary history or ecological opportunity to learn to fear this predator species. As such, bullfrogs show responses to species-specific fish predators and do not generalize across predatory fish. Recognition trials testing response to a fish predator that is taxonomically similar to largemouth bass, such as the smallmouth bass (*M. dolomieu*), will further expand on this question of generalized threat responses.

We found that wild-caught individuals did not respond as strongly to largemouth bass chemical cues as laboratory-reared individuals. While the response was not statistically significant, it begs the question whether largemouth bass are an important predator in this system. Threat-sensitive predator avoidance dictates that antipredator responses should reflect species-specific predation risk (Semlitsch & Reyer 1992; Gherardi et al. 2011). For example, wood frog (*Rana sylvatica*) tadpoles adjust response based on predator type and risk intensity (Ferrari & Chivers 2009b; Ferrari et al. 2009). Similarly, Epp & Gabor (2008) found that laboratory-reared San Marcos salamanders (*Eurycea nana*) responded to a sympatric non-native predator, but that wild-caught individuals did not. They concluded that experience allowed individuals to effectively gauge risk and limit costly behaviors such as immobility. Bullfrog individuals with largemouth bass experience may be weighing this species-specific risk as less important relative to other predators or environmental pressures, such as invertebrates or pond drying (Welborn et al. 1996). Bullfrog tadpoles can be unpalatable to some fish predators; this can protect populations occupying communities with predators that avoid bullfrog tadpoles and selectively forage on alternative prey (Kruse & Francis 1977). As such, it is necessary to test for palatability when assessing predator/prey relationships.

Interestingly, ontogenetic timing of predator exposure influenced behavioral response (i.e., wild-caught vs. laboratory-reared). Laboratory-reared individuals from populations sympatric with fish predators retained the ability to recognize that predator at a later developmental stage. This latent behavioral plasticity may be an epigenetic response as predator chemical cues in the environment resulted in plastic changes in individual phenotypes (Hallgrimsson & Hall 2011). Mandrillon & Saglio (2009) found that administering predator chemical cues during the embryo stage in the Common frog (*Rana temporaria*) allowed tadpoles to respond appropriately to predator risk. The heritability of this response was not tested in this study; thus, we can only hypothesize as to the epigenetic implications of behavioral plasticity as a

function of predator community and ontogeny. Further studies are needed to explore the genetic, epigenetic, and plastic antipredator responses in invasive bullfrog populations (Ghalambor et al. 2007; Ferrari & Chivers 2009a).

Finally, we hypothesized that exposure to a predator chemical cue treatment in which the predators had been fed conspecifics would increase refuge use in tadpoles owing to the presence of diet cues. Neither the sympatric nor allopatric populations responded more intensely to predators when species-specific chemical cues were accompanied by predator diet cues. Diet pheromones can be indicative of danger, but they are also unreliable at indicating degree of risk (Kats & Dill 1998). Additionally, the concentration of diet cues in our two experiments may have been too low to elicit a response as low concentrations can be perceived as low risk (Ferrari & Chivers 2006; Kesavaraju et al. 2007). Manipulations of cue type and concentration could help to parse out the relative importance of cues at indicating risk.

This study suggests that freshwater habitats with diverse predator communities may be more biological resistant to invasion from the American bullfrog. We found that inexperience with fish predators can result in ineffective response to species-specific chemical cues in at least one bullfrog population within the Pacific Northwest invasion range. Invasive populations can suffer increased predation rates because of inexperience with predators (Verhoeven et al. 2009). For example, invasive American bullfrog populations are the preferred prey item of the native red-banded snake in China (Li et al. 2011). Similarly, invasive bullfrogs in Oregon may be preferred prey for many native predators. We posit that if bullfrogs can lose the ability to recognize historical predators, perhaps predators that temporally and spatially vary across a landscape are perceived as novel predators (Kishida et al. 2007). Freshwater habitat matrices connected to the floodplain and capable of supporting a diverse suite of migrating invertebrate and vertebrate predators may have greater resistance to bullfrog invasion relative to simplified pond and wetland communities. This argues for habitat connectivity, maintenance of native biodiversity, and the removal of invasive species that negatively impact native predator communities.

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