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ORIGINAL PAPER

Shared behavioral responses and predation risk of anuran larvae and adults exposed to a novel predator

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Abstract Invasive species are a regional and global threat to biological diversity. In order to evaluate an invasive predator species' potential to harm populations of native prey species, it is critical to evaluate the behavioral responses of all life stages of the native prey species to the novel predator. The invasion of the African clawed frog (*Xenopus laevis*) into southern California provides an opportunity to evaluate the predation risk and behavioral responses of native amphibians. We performed predation trials and explored prey behavioral responses to determine how this invasive predator may impact native amphibian populations using Pacific chorus frogs (*Pseudacris regilla*) as a representative native California prey species. We found that *X. laevis* will readily prey upon larval and adult life stages of *P. regilla*. Behavior trials indicated that both larval and adult *P. regilla* exhibit prey response behaviors and will spatially avoid the novel invasive predator. The results suggest that native anurans may have a redundant predator response in both the larval and adult life stages, which could reduce the predatory impact of *X. laevis* but also drive emigration of native amphibians from invaded habitat.

Keywords Predator–prey interactions · Complex life cycle · African clawed frog · *Xenopus laevis* · *Pseudacris regilla*

Introduction

Invasive species threaten biodiversity worldwide and reduce or even eliminate populations of native species (Mack et al. 2000; Bellard et al. 2016). Amphibians, in particular, have suffered severe population losses from invasive species owing to disease transmission, competition, habitat alterations, and direct predation (Kats and Ferrer 2003; Bucciarelli et al. 2014). Although many prey taxa have evolved the capacity to detect and respond to the presence of their natural predators to reduce predation risk, naïve native prey species may lack the ability to recognize or effectively respond to introduced predatory species (Sih et al. 2010). A native species may not respond appropriately, particularly if the exotic predator is not closely related to the animal's native predators (Ferrari et al. 2010). Novel invasive predatory species such as introduced mammalian predators in New Zealand (Innes et al. 2010; Goldson et al. 2015) and introduced snakes in Guam (Fritts and Rodda 1998; Wiles et al. 2003) can cause precipitous loss of native species. Similarly, native amphibians in parts of the western United States have declined or disappeared owing to the introduction of

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predatory bullfrogs and fish species (Knapp and Matthews 2000; Adams and Pearl 2007).

Although studies have explored the responses of anurans to a suite of invasive species to determine if the native species respond to novel predators (e.g. (Gall and Mathis 2010; Nunes et al. 2012; Pease and Wayne 2013), these studies have focused on a single anuran life stage, either the adult or larval stage. But in each life stage the species may be adapted to detect and evade different predators. As a consequence, it is important to include both larval and adult anuran life stages when evaluating the impact of an invasive species because one life stage may be more vulnerable to predation or less able to respond to the novel predator than the other.

The African clawed frog (*Xenopus laevis*) invasion into southern California (Crayon 2005) offers an opportunity to investigate the responses of native anurans to a novel predatory species through their life cycle. As a generalist predator that preys on its own eggs and larvae (McCoid and Fritts 1980; Measey and Tinsley 1998) *X. laevis* adults could potentially attack and prey upon native amphibian eggs, larvae and adults. Larval *X. laevis,* on the other hand, are not considered a predatory threat to native amphibians because they are obligatory filter feeders (Seale 1982) and were therefore not included in this study. Native to sub-Saharan Africa (Tinsley et al. 1996), the invasion of *X. laevis* into southern California has coincided with declines in native amphibians (Mahrdt and Knefler 1972; McCoid and Fritts 1980); however, it is not clear if *X. laevis* predation was a factor in these declines (Crayon 2005).

Of the dietary studies involving invasive *X. laevis* populations (McCoid and Fritts 1980; Measey 1998; Lobos and Measey 2002; Faraone et al. 2008; Lillo et al. 2011), only one study has shown that *X. laevis* will consume native amphibians (Amaral and Rebelo 2012). Few of these studies, however, reported the presence of native amphibians in the ponds where *X. laevis* were collected (McCoid and Fritts 1980; Measey 1998; Lillo et al. 2011). One study in Italy showed that several amphibian species (*Hyla intermedia*, *Pelophylax esculentus*, *Discoglossus pictus*), but not all species (*Bufo bufo*), stopped reproduction in ponds after *X. laevis* had established (Lillo et al. 2011). This suggests that native anurans that are susceptible to predation either emigrate from invaded waters to avoid predation or are quickly consumed, resulting in local extirpation.

Southern California amphibians have co-evolved with a variety of native anuran predators. For example, adult California red-legged frogs (*Rana draytonii*) are known to prey upon Pacific chorus frogs (*Pseudacris regilla*) (Hayes and Tennant 1985) and southern mountain yellow-legged frogs (*Rana muscosa*) are thought to feed on *P. regilla* and *Anaxyrus* (*Bufo*) species (Pope and Matthews 2002). *Xenopus laevis* is comparable in size to these predatory anurans, but belongs to a family (*Pipidae*) that is not native to North America, which leaves a long evolutionary gap for potential prey recognition. Invasive *X. laevis* are also not typical of California frogs because they are nearly fully aquatic, leaving water only occasionally for dispersal (Lobos and Jaksic 2005). Their lack of tongue and suction feeding strategy are more typical of a fish than a native amphibian (Measey 1998). *Pseudacris regilla* do respond to fish predators (Pearl et al. 2003) but may not associate novel amphibian cues with a fish-like predatory threat. As a consequence, native amphibians may not recognize or appropriately respond to *X. laevis* in their adult or larval life stages.

This study used Pacific chorus frogs (*Pseudacris regilla*) as a representative of native California species to explore potential predation by and behavioral responses to *X. laevis*. *Pseudacris regilla* was chosen because it is highly palatable to most predators, is common throughout southern California, and has declined in areas *X. laevis* has invaded (Mahrdt and Knefler 1972; McCoid and Fritts 1980). Given that both larval and adult *P. regilla* occupy the slow-moving aquatic habitats favored by *X. laevis* (Crayon 2005), it is important to evaluate the potential effect of *X. laevis* on both larval and adult *P. regilla* life stages.

The following experiments were designed to determine (1) whether *X. laevis* prey upon *P. regilla* larvae and adults and (2) whether *P. regilla*, larvae or adults, respond to *X. laevis* with anti-predator behavior. Understanding the predation risks and responses will serve as a first step towards assessing the impact *X. laevis* may have on native anurans, and the potential for coexistence of native anurans with *X. laevis*.

Materials and methods

Experiments were performed over two summer field seasons using animals collected from the wild. The *P.*

regilla and *X. laevis* were kept in plastic aquaria (18 cm wide, 17 cm tall, 28 cm long), filled with 4L of Nestle® bottled drinking water for adult *X. laevis*, larval *X. laevis*, and larval *P. regilla*, whereas adult *P. regilla* were supplied a water dish, unless otherwise stated. Animals were fed twice per week and tanks were cleaned weekly. Larval *P. regilla* were fed flake fish food and algal pellets; adult *P. regilla* were fed live crickets; and adult *X. laevis* were fed *Xenopus*-specific Nasco® frog brittle.

Xenopus laevis predation on larval *P. regilla*

Laboratory experiments were performed to determine if adult *X. laevis* would feed on larval *P. regilla*. The *P. regilla* larvae were raised from egg clutches deposited in the laboratory containers by amplexed adult pairs collected from Atascadero Creek, Santa Barbara County. Nine adult *X. laevis* were collected from a pond in the Hedrick Ranch Nature Area (HRNA), which is adjacent to the Santa Clara River, Ventura County, and kept in laboratory aquaria. One adult *X. laevis* was excluded from the study because it had not been observed feeding in the days leading up to the experiment and may have been sick at capture or particularly distressed from captivity.

The eight remaining *X. laevis* were fasted for 5 days and measured (snout-to-vent length, SVL) before the predation trials. A *P. regilla* larva (stages 32–41) (Gosner 1960) was haphazardly selected and placed in one of the eight *X. laevis'* tanks. When the *X. laevis* consumed a *P. regilla*, another larva was placed in the tank within 5 min. The *P. regilla* were continuously replaced if consumed. Each trial ended when the *X. laevis* did not consume the *P. regilla* larva within 10 min of its introduction. We analyzed the relationship between the size of each *X. laevis* and the number of *P. regilla* it consumed using a linear regression.

Xenopus laevis predation on adult and juvenile *P. regilla*

A laboratory experiment was performed to determine if adult *X. laevis* would feed on adult and juvenile *P. regilla*. The eight adult *P. regilla* used in this experiment were collected from Atascadero Creek, Santa Barbara County. The juvenile *P. regilla* were the remaining metamorphosed larvae from the previous *P. regilla* larva predation experiment never exposed to a *X. laevis*. The sixteen *X. laevis* were collected from the isolated pond at the HRNA, eight of which had been used in the previous larval *P. regilla* predation experiment.

The *X. laevis* were fasted for 2 days before the trials. One *X. laevis* and one adult or juvenile *P. regilla* were measured and placed in an aquarium (18 cm wide, 17 cm tall, 28 cm long) filled with 5.5 L of bottled water with approximately 4 cm of space between the water surface and a fine mesh lid. The *X. laevis* were evaluated based on whether or not the *P. regilla* was consumed within a 24 h period. Two *X. laevis* that did not consume a *P. regilla* were re-tried with smaller *P. regilla*.

Behavioral response of larval *P. regilla* to *X. laevis* and a native invertebrate predator

A laboratory experiment was performed to determine if *P. regilla* larvae would exhibit an anti-predatory behavioral response in the presence of adult *X. laevis* (a non-native predator) and dragonfly nymphs (Aeshnidae; a native predator) as measured by larval activity levels and spatial avoidance. The *P. regilla* larvae were collected from a shallow isolated artificial pool lacking predators located in the HRNA, then kept in an aerated 20 gallon glass aquarium at 24 °C. Four of the *X. laevis* were collected from a pond on HRNA and four from an isolated pool on Piru Creek, a tributary of the Santa Clara River, in Ventura County. The four *X. laevis* collected from HRNA were later used in the *P. regilla* predation experiments. Eight dragonfly nymphs were collected from an isolated pool on the UCSB campus and kept in the laboratory in individual aerated plastic containers with 0.5 L of bottled water and fed bloodworms twice a week.

Trials were performed in clear plastic aquaria (18 cm wide, 17 cm tall, 28 cm long), each divided into two equal chambers by a clear plastic mesh divider (1.5 mm gauge). The tanks' sides were covered in a white translucent screen to reduce shadows. Four liters of fresh bottled water at 25 ± 1.5 °C were used in each trial. Tanks were wiped down with 10% bleach and rinsed repeatedly (approximately five times) with DI water between each trial to remove residual animal cues.

A *P. regilla* larva was placed into each of the five treatments: *X. laevis* present (n = 22), *X. laevis* scent (n = 24), dragonfly present (n = 26), dragonfly scent (n = 18), or a control (no predator or predator scent; n = 25). In the *X. laevis* and dragonfly present treatments, the predator was placed in the trial aquaria for 30 min and the water was stirred prior to the introduction of the *P. regilla* larva to the opposing chamber. In the *X. laevis* and dragonfly scent treatments, the predator was placed in the aquarium for 30 min, removed, and the water stirred prior to the introduction of the *P. regilla* larva to the opposing chamber. Each *P. regilla* larva was staged following Gosner (1960) and used only once. The *X. laevis* adults and dragonfly nymphs were used repeatedly in trials.

Trials were conducted between 1100 and 1600 h and each ran for 11 min. The trials were videotaped from 20 cm above the water using a digital camera and later analyzed to evaluate *P. regilla* activity levels and spatial distribution within the aquarium. The first minute of each trial was discarded as an acclimation period for the *P. regilla* larva. In the following 10 min, we summed the number of seconds each *P. regilla* larva was active and the number of seconds it spent in the half of the aquarium closest to the mesh divider. Larvae were considered active if their tails were in motion. All time measurements were rounded to the nearest second for each bout of activity or move from one half of the aquarium to the other.

Separate ANOVAs and post hoc Tukey tests were performed on the number of seconds the *P. regilla* were active and the number of seconds they spent on the half of the tank closest to the mesh divider to compare treatment effects on activity levels and spatial avoidance, respectively.

Behavioral response of adult *P. regilla* to *X. laevis*

A field enclosure experiment was performed to determine if adult *P. regilla* would spatially avoid adult *X. laevis*. Thirty new adult *P. regilla* were collected from Isla Vista and Atascadero Creek, Santa Barbara County. Twenty new adult *X. laevis* were collected from a pond on HRNA.

Fifteen enclosures were used in the field experiment (Fig. 1). Each enclosure consisted of a rectangular 3-dimensional PVC frame (45 cm wide, 22 cm tall, 58 cm long) with small gauge (1 cm) plastic mesh on the top and on the four sides. The bottom of the enclosure was natural dirt with two aquaria (18 cm wide, 17 cm deep, 28 cm long) buried flush with the ground and filled with 7 L of well water, acting as separate water bodies. The two aquaria were arranged in the enclosure to create two halves, each with a water source and equal areas of substrate.

Fifteen enclosures, five control without *X. laevis* and ten treatment enclosures with *X. laevis* were placed, single file, in an open area in HRNA, with every third enclosure a control. One adult *P. regilla* was included in each treatment and control enclosure. In each treatment enclosure, one *X. laevis* was placed in a mesh cube (20 cm by 15 cm by 15 cm) in the aquarium on one side of the enclosure, and an empty mesh cube was placed in the aquarium on the other side (alternating sides in each treatment enclosure). In this way, the *X. laevis* was confined to the mesh cube in one of the aquaria in the treatment enclosures but the *P. regilla* had free movement within the entire enclosure and could use either of the aquaria as a water source.

The experiment was run twice, each for 6 days, first with all male *P. regilla* and the second with all female *P. regilla*. Different *X. laevis* were used in each run of the experiment. At the beginning of the experiment, the *P. regilla* was placed in the center of each enclosure 30 min after a *X. laevis* had been placed in the mesh aquarium cube in each treatment enclosure. The position of each *P. regilla* was recorded three times per 24 h, once at dusk, once in the middle of the night at 0100 h and once at pre-dawn. The experiments began at 0100 h on the first day and ended with a pre-dawn observation on the sixth day, for a total of 17 observation periods. Each enclosure was checked in succession and no more than 3 min was spent locating the *P. regilla* in each enclosure.

The data were statistically analyzed with sign tests based on which side of the enclosure each individual *P. regilla* preferred. For each *P. regilla*, we summed the number of times it was observed on each side of the enclosure: the non-*X. laevis* or *X. laevis* side of the enclosure for the treatments; or the East or West side of the enclosure for the controls. We assigned a preference for one side or the other based on which side of the enclosure the *P. regilla* was observed on more often. Similarly, an additional sign test was performed to determine a preferential use of either of the water sources within the control and treatment enclosures using only the observation points when *P. regilla* were observed in the water.

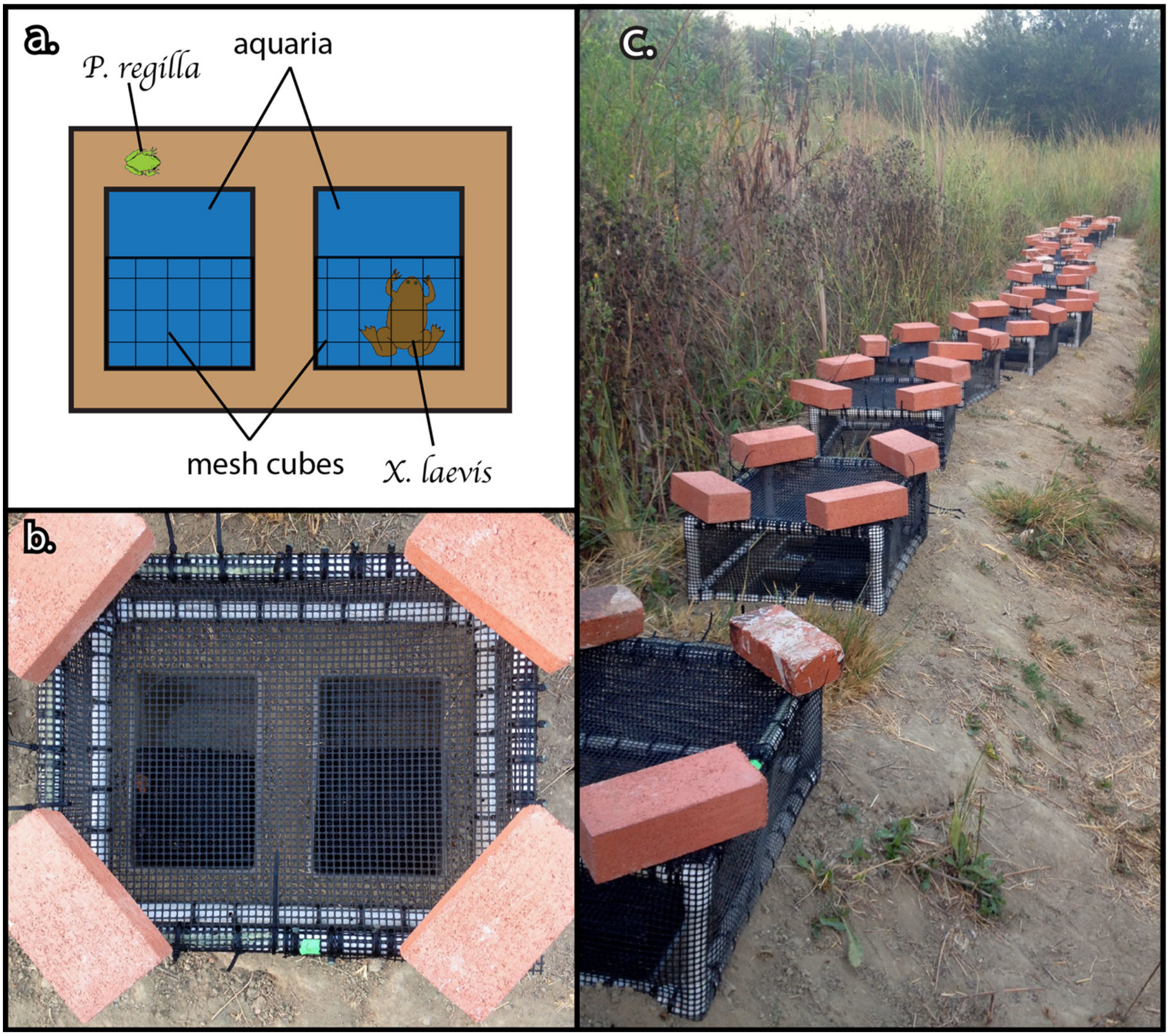


Fig. 1 A diagram showing an overhead view of the inside of a treatment enclosure with a *X. laevis* penned in the right aquarium and the *P. regilla* on the opposite (non-*X. laevis*) side of the enclosure (**a**); a top view of a treatment enclosure (**b**); the 15 enclosures set up in the field (**c**). Bricks were used to hold the enclosures in place

Results

Xenopus laevis predation on larval *P. regilla*

There was a significant positive correlation between the size of the *X. laevis* and the number of *P. regilla* larvae consumed (linear regression, $R^2 = 0.83$, $p < 0.05$) (Fig. 2). Seven out of the eight adult *X. laevis* consumed at least one *P. regilla* larva during the trial. One *X. laevis* individual consumed 25 *P. regilla* larvae in the time of the experiment, approximately 3.5 h.

Xenopus laevis predation on adult and juvenile *P. regilla*

The *X. laevis* consumed 15 of the 18 adult and juvenile *P. regilla* within the 24-h feeding trials (Fig. 3). All juvenile *P. regilla* (SVL between 14 and 24 mm) were

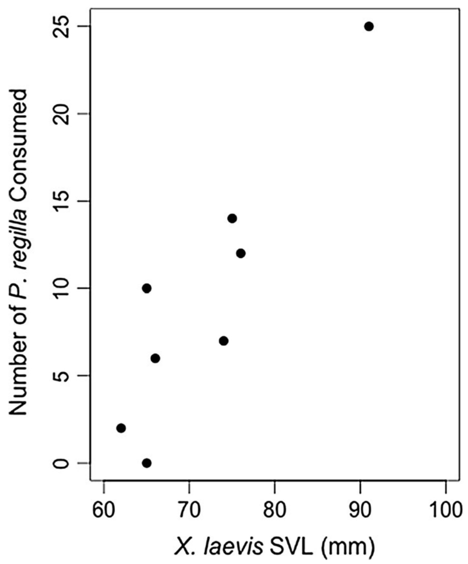


Fig. 2 The number of *P. regilla* larvae (Gosner stage 32–41) consumed by each *X. laevis* in the approximately 3.5 h predation trial (*SVL* snout to vent length)

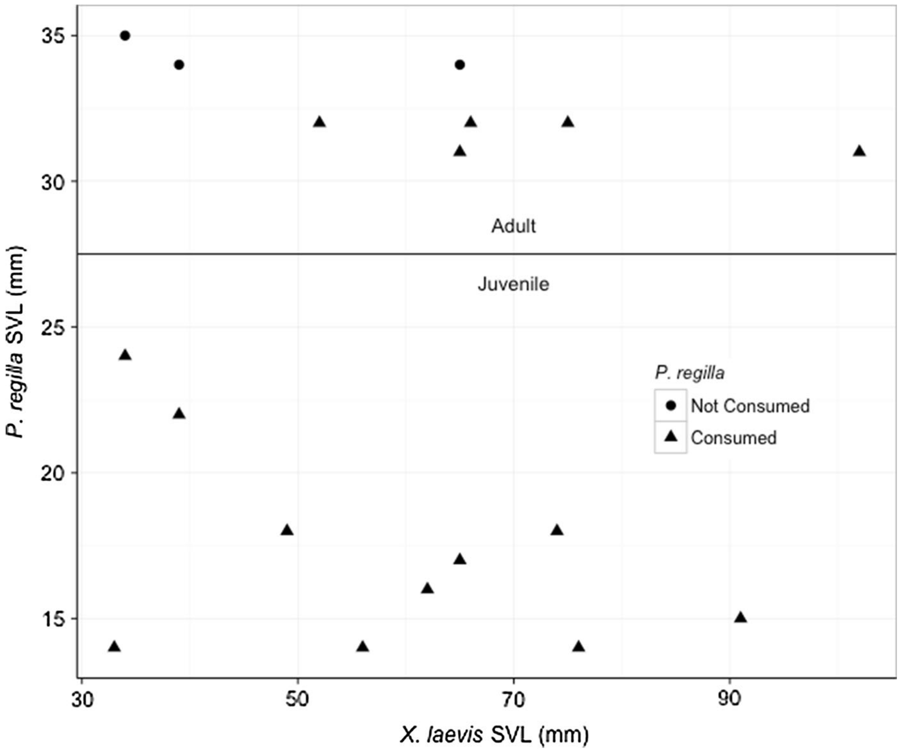
consumed by *X. laevis* (SVL 33–102 mm). The three largest adult *P. regilla* (SVL 34–35 mm) were not consumed.

Behavioral response of larval *P. regilla* to *X. laevis* and a native invertebrate predator

There was a significant effect of predator treatment on *P. regilla* larvae activity levels (ANOVA: $F_{1,4} = 4.25$, $p < 0.01$). However, no activity levels in any of the treatment were found to be significantly different from the control. The post hoc analysis found significant differences only between the *X. laevis* scent treatment and both the dragonfly nymph present and dragonfly nymph scent treatments (Fig. 4) (Tukey HSD, $p < 0.05$). For both *X. laevis* and dragonflies there is a trend for increased activity in the presence of the predator compared to the presence of only the scent of the predator; however, these differences are not statistically significant for either predator species.

There was a significant effect of predator treatment on spatial distribution of larval *P. regilla* within the aquaria (i.e. on the time spent in the half of the aquarium closest to the mesh divider vs. the back half of the aquarium; ANOVA: $F_{1,4} = 3.57$, $p < 0.001$). The post hoc analysis found significant differences between the control and the *X. laevis*-present treatment, with the *P. regilla* spending significantly less

Fig. 3 Consumption of adult and juvenile *P. regilla* by *X. laevis* of various sizes in a 24-h predation trial (*SVL* snout to vent length)



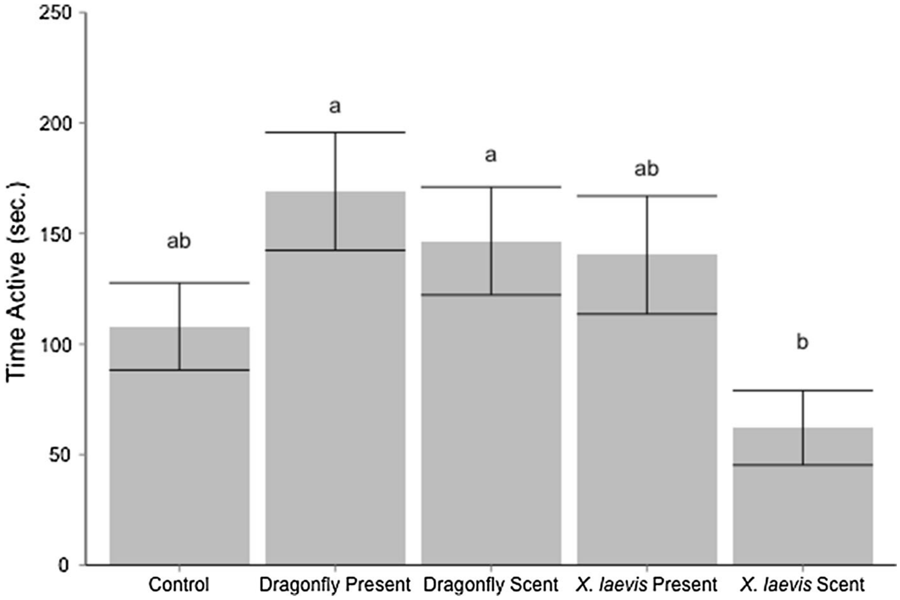


Fig. 4 Activity levels (mean ± SE) of the *P. regilla* larvae when exposed to the scent cues or presence of a dragonfly nymph or adult *X. laevis*. *Letters* above SE *bars* distinguishing statistical differences between treatments and/or the control (Tukey pairwise comparison, $p < 0.05$)

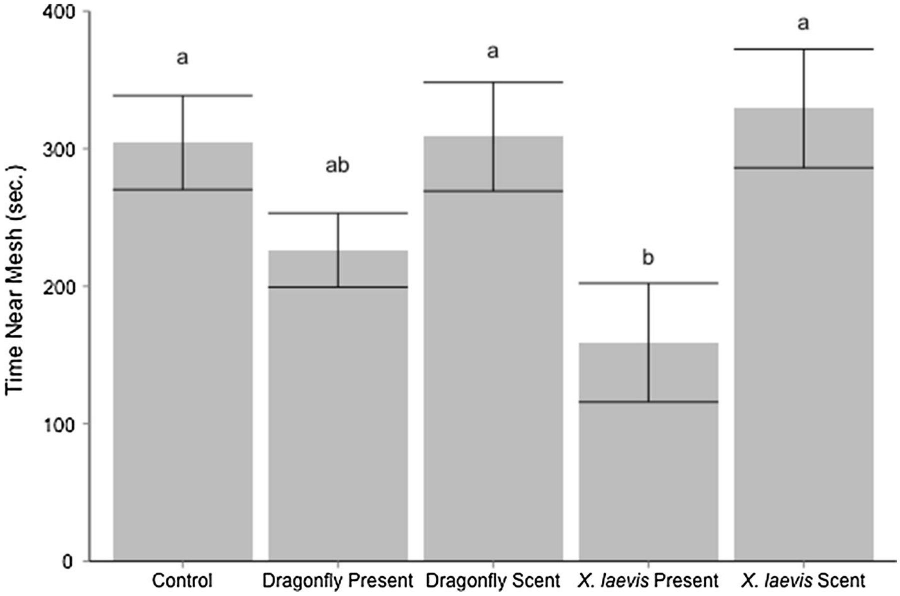
time in the half of that aquarium that was closer to the predator (Fig. 5; Tukey HSD, $p < 0.05$).

Behavioral response of adult *P. regilla* to *X. laevis*

Adult *P. regilla* in the absence of *X. laevis*, displayed no preference for either side of the enclosures (binomial test: n = 10, $p > 0.05$) (blue dots in Fig. 6a). Five *P. regilla* in the control enclosure were observed more often on the East side and five were observed more often on the West side of the enclosure. All control *P. regilla* were observed at every survey period.

Pseudacris regilla in the treatment enclosures displayed a significant preference for the side of the

Fig. 5 Spatial distribution of the *P. regilla* larvae when exposed to the scent cues or presence of a dragonfly nymph or adult *X. laevis*; number of seconds (mean ± SE) the *P. regilla* larvae spent on the half of the aquarium closest to the center mesh divider (near the predator). *Letters* above the SE *bars* distinguishing statistical differences between treatments and/or the control (Tukey pairwise comparison, $p < 0.05$)



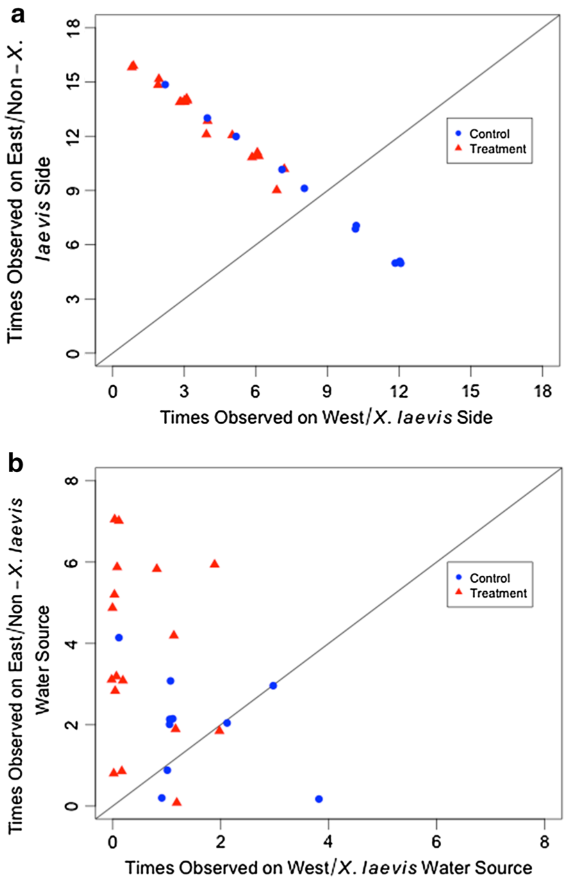


Fig. 6 The number of times each adult *P. regilla* was observed on either side of the enclosure (**a**) or in the water sources (**b**). *Pseudacris regilla* in control enclosures were observed on either the East or West side and *P. regilla* in treatment enclosures were observed on either the non-*X. laevis* or the *X. laevis* side. Points were offset slightly to distinguish individuals with identical observation counts. The *diagonal line* represents an equal number of observations on either side of the enclosure or water source

enclosure without the *X. laevis* (binomial test: n $= 20$, $p < 0.001$) (red triangles Fig. 6a). All 20 *P. regilla* in the treatment enclosures were observed more often on the non-*X. laevis* side of the enclosure than the *X. laevis* side. The *P. regilla* moved throughout the enclosure, rarely observed in the same location for two sequential time points in the treatment or control enclosures. On two occasions, a *P. regilla* in a treatment enclosure could not be located within the enclosure and those individual *P. regilla* have 16 rather than 17 observations.

The *P. regilla* also displayed a significant preference for the non-*X. laevis* water source in the treatment enclosures (binomial test: n $= 16$, $p < 0.001$) and showed no preference for the East or West water sources in the control enclosures (binomial test: n $= 8$, $p > 0.05$) (Fig. 6b). *Pseudacris regilla* that were not observed in water or were observed an equal number of times in both water sources were not included in this statistical analysis. There does not appear to be a pattern for when the *P. regilla* were observed in the *X. laevis* water source; some individuals were observed in the *X. laevis* water source in the beginning, middle, and end of the experiment. Only one female *P. regilla* was observed in a *X. laevis* water source, on one occasion, whereas five males were observed a total of seven times in *X. laevis* water source.

Discussion

Our predation experiments suggest that invasive *X. laevis* will prey upon larval and adult *P. regilla*. This is unsurprising given that larval *P. regilla* are a similar size to *X. laevis* larvae, which are cannibalized (Tinsley and McCoid 1996). Of greater concern for native amphibian populations is the ability of *X. laevis* to consume the adult *P. regilla*, which may have more profound population consequences. The loss of later life stages and older reproductive individuals may cause greater declines in populations than the loss of eggs or young juveniles (Doak et al. 1994; Vonesh and la Cruz 2002). Larval anurans suffer high mortality rates, some over 95% (Herreid and Kinney 1966), which means the few that survive to reproductive age become increasingly important to create the next generation. Only the largest adult *P. regilla* (34–35 mm SVL) avoided predation when matched up with small *X. laevis* (<70 mm SVL), presumably owing to gape limitation of the smaller adult *X. laevis*. However, gape limitation is unlikely to limit the larger *X. laevis* that reach >100 mm (SVL).

Although larval and adult *P. regilla* life stages were consumed by *X. laevis* in the laboratory, this does not necessarily imply that *X. laevis* predation will reduce or extirpate *P. regilla* populations in the field, although there is some evidence of this occurring (Mahrdt and Knefler 1972; McCoid and Fritts 1980). Amphibians can reduce their detection and capture by predators through a variety of anti-predator behaviors. Laval amphibians exhibit spatial avoidance, increased refuge use, as well as changes in morphology, timing of metamorphosis, and activity level (Skelly and Werner 1990; Pearl et al. 2003; Hossie et al. 2010). Similarly adult anurans are selective in where they lay their eggs and have been shown to avoid ovipositing in waters with predators (Rieger et al. 2004). These anti-predator responses should be expressed only in the presence of a threat because the behaviors or changes in morphology tend to be costly. For example, reduced larval activity reduces the amount of time larvae spend foraging and thereby adversely affects their later size, survivorship, growth, and development (Skelly 1992).

In this study, *P. regilla* displayed a spatial avoidance response to predator presence but did not display changes in activity levels. It is not surprising that the larvae displayed only one of the two response behaviors tested. Anuran larvae have been shown to have specific responses for different predators (Relyea 2001) and often the presence of more predator cues results in a stronger prey response than one predator cue alone (Hettyey et al. 2012). The *X. laevis* scent cue may trigger a response that was not measured in this study, such as changes in tail morphology or accelerated time to metamorphosis.

The larvae's spatial avoidance response likely results from general predator cues that happen to fit *X. laevis* rather than cues specific only to *X. laevis*. The changes in water movement or an approaching dark shape could have caused the *P. regilla* to respond to the presence of *X. laevis*. There were multiple occasions when the predator appeared to have observed the *P. regilla* larva on the other side of the mesh and lunged towards it, which often caused the *P. regilla* to quickly swim away. This predator behavior could have influenced the spatial distribution of the *P. regilla* larvae because it only occurred near the mesh divider.

Predator motion could also explain the differences seen in the activity level between the predator present and predator scent-only treatments. For both *X. laevis* and dragonflies as predators, there was a tendency for *P. regilla* larvae to be more active in the presence of the predators than in the presence of just the predator scent. The motion of the predator appeared to be necessary for the *P. regilla* to initiate a behavioral response. The *P. regilla* did not appear to respond to the visual outline of the *X. laevis* as a potential threat; the larvae would often approach a motionless *X. laevis* or rest immediately next to the *X. laevis* on the opposite side of the mesh divider.

Xenopus laevis may be too far removed evolutionarily from *P. regilla's* natural predators, for *P. regilla* to recognize its specific scent or other *X. laevis*-specific cues as a potential threat. Although *P. regilla* did evolve with native anuran predators (Hayes and Tennant 1985; Pope and Matthews 2002), more distantly related animals are thought to have more dissimilar scent cues that limit an amphibian's ability to recognize novel predators (Ferrari et al. 2010). This has been shown with other amphibian species when exposed to novel predatory fishes with varying relatedness to their native predators (Gall and Mathis 2010). The Pipidae family, which includes *X. laevis*, is native to Africa and South America and *Xenopus* is endemic to sub-Saharan Africa (Tinsley and Kobel 1996). The olfactory scent cues may not be recognized by *P. regilla* larvae, which could force the larvae to rely upon more general predator cues that matched a native predator in some way. Native predatory anurans (*R. draytonii* or *R. muscosa*) were not included in this study due to their sensitive population statuses, and no other study was found to explore the behavioral responses of *P. regilla* to native anuran predatory species.

It is unclear why *P. regilla* larvae did not respond significantly to the native dragonfly nymphs, a native predator. Other anuran species have displayed reduced activity levels in the presence of native dragonfly nymphs (Nunes et al. 2012), and *P. regilla* larvae have been shown to spatially respond to dragonfly nymphs (Hammond et al. 2007). In our study, the data suggest that *P. regilla* larvae may increase their activity levels and spatially avoid dragonfly nymphs when in their presence, perhaps in effort to leave the area. However, the increased activity did not significantly differ from the control and may be a product of the attack motions of the nymphs eliciting flight reactions from the larvae.

Larval *P. regilla* might have exhibited stronger responses to the presence of the dragonfly and *X. laevis* predators were the scent of a consumed conspecific present. Anuran larvae sometimes respond to novel predators when a cue from consumed conspecifics is present, either through the diet of the predator or the presence of the larvae's broken skin (Marquis et al. 2004; Mandrillon and Saglio 2005). This response could compensate for the lack of a species-specific predator response, allowing native larvae to avoid a range of predators without recognizing them individually. Neither predator in this experiment was fed anurans as part of their diet in order to eliminate this as a potential factor, but it may be key to stimulating a behavioral response.

Adult *P. regilla* displayed a significant spatial avoidance behavior when exposed to *X. laevis*. The adult behavioral response may be more important than the larval response because the adults can reduce the larvae's exposure to the *X. laevis* by discriminating between invaded and non-invaded sites when selecting breeding sites. If the parents avoid depositing eggs in areas with aquatic predators, then the larvae have less need for an innate anti-predator response because they are not frequently exposed to those predators. Other naïve anuran species in Europe have been shown to stop reproduction in ponds after establishment of invasive *X. laevis* (Lillo et al. 2011). The data from the field enclosure experiment suggests that *P. regilla* avoid *X. laevis* invaded water sources when possible, because *P. regilla* were rarely observed in the water with a penned *X. laevis*. This experiment was performed during the breeding season of *P. regilla*, which suggests that *P. regilla* may avoid *X. laevis* areas when ovipositing, if alternative sites were available.

Xenopus laevis displays a clear ability to consume both larval and adult stages of native amphibians and may indirectly cause native amphibian emigration from local habitats through spatial predator avoidance. Native California anurans are absent from many areas that *X. laevis* has invaded but have never been found in the stomach contents of *X. laevis* (Crayon 2005), suggesting either quick consumption to extirpation or emigration of native anurans from those areas. These potential impacts may warrant *X. laevis* management to limit their current populations and prevent further invasions. Active management aimed at preventing their introduction is ideal because they are difficult to eradicate once established (Crayon 2005), although *X. laevis* populations have been shown to decline or go extinct on their own due to extreme cold or dry weather conditions (Rebelo et al. 2010; Tinsley et al. 2015). The recent drought in southern California may have eliminated some populations as semi-permanent water sources dried. Further study will be necessary to determine if co-existence between native amphibians and *X. laevis* occurs in the wild.

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