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Palatability and Antipredator Response of Yosemite Toads (*Anaxyrus canorus*) to Nonnative Brook Trout (*Salvelinus fontinalis*) in the Sierra Nevada Mountains of California

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In the Sierra Nevada Mountains of California, Yosemite Toads (*Anaxyrus canorus*) have declined throughout their range where Brook Trout (*Salvelinus fontinalis*) have been widely introduced. Amphibians that evolved in fishless habitats often lack the necessary chemical defenses and behavioral responses to avoid predation. True Toads (family Bufonidae), however, possess noxious chemicals that often deter predators. Our goal was to test whether eggs, tadpoles, and postmetamorphic toads of *A. canorus* are a palatable food source for *S. fontinalis*, assess the antipredator behavior of tadpoles of *A. canorus* by exposing them to various predator chemical cues, and determine sublethal effects on three lifestages of *A. canorus* from sampling by *S. fontinalis*. We found that eggs, tadpoles, and postmetamorphic toads of *A. canorus* exhibit absolute unpalatability to *S. fontinalis*. In addition, tadpoles of *A. canorus* did not exhibit a significant difference in behavior when exposed to chemical stimuli. Moreover, observational experiments revealed that trout would sample, then reject lifestages of *A. canorus* unharmed, while trout readily consumed tadpoles of Pacific Chorus Frog (*Pseudacris regilla*). We therefore infer that early lifestages of *A. canorus* likely possess existing chemical defenses as a result of interactions with native predators that adequately protect them from nonnative trout predation. Although trout removal often leads to the recovery of other Sierra Nevada amphibian populations, trout removal would likely have no effect on populations of *A. canorus* given our results. Therefore, we suggest that other factors thought to be contributing toward *A. canorus* decline should be investigated before efforts are concentrated on removing trout from toad habitats.

WORLDWIDE, amphibians are declining faster than any other group of vertebrates. Declines have been attributed to disease (Daszak et al., 2003), introduction of alien species (Kats and Ferrer, 2003), habitat loss (Stuart et al., 2004), climate change (Pounds et al., 2006), pesticides (Davidson, 2004; Reylea, 2005), as well as the synergistic effects of these stressors (Davidson and Knapp, 2007). Bufonids in particular, appear to be declining at a faster rate than any other amphibian family (Stuart et al., 2004). The practice of introducing nonnative fish into fishless habitats for recreational or other purposes often results in the decline of native amphibian assemblages (Kats et al., 1988; Knapp, 1996; Kats and Ferrer, 2003). Historically, the Sierra Nevada Mountains of California were almost entirely fishless above 1,800 meters (6,000 feet; Knapp, 1996). Native to the Eastern U.S. and Canada, Brook Trout (*Salvelinus fontinalis*) have been introduced throughout the Sierra Nevada using pack stock and aerial stocking techniques (Leitritz, 1970). The introduction of trout into the Sierra Nevada has been shown to have negative effects on native amphibians such as the Pacific Chorus Frog (*Pseudacris regilla*; Matthews et al., 2001) and the endemic Mountain Yellow-Legged Frog complex (*Rana muscosa* and *R. sierrae*), the latter of which has declined from over 90% of its historical range (Bradford et al., 1994; Knapp and Matthews, 2000; Vredenburg, 2004). *Anaxyrus canorus* is another declining Sierra Nevada endemic amphibian (Sherman and Morton, 1993), although it has been unclear whether introduced trout were also contributing toward this decline. There have been few experimental attempts to determine if an amphibian's existing antipredator defenses are sufficient to protect them from predation by nonnative fish.

There is no good evidence for the extirpation of *A. canorus* from water bodies containing trout due to the lack of range-wide historical data for *A. canorus*. Even field observations have been confounding. For example, *S. fontinalis* have been observed to pick at eggs and tadpoles of *A. canorus* (D. Martin, pers. comm., 2003), while other observers have witnessed *S. fontinalis* actively avoiding tadpoles of *A. canorus* (R. Knapp, pers. comm., 2003). Stomach contents of *S. fontinalis* from sites with eggs and tadpoles of *A. canorus* contained invertebrate prey items only (R. Grasso, unpubl. data). Bufonids are known to possess noxious skin substances (Flier et al., 1980; Daly, 1995) that often make them distasteful to predators, while ranid and hylid species appear to be more susceptible to predation (Voris and Bacon, 1966; Kruse and Stone, 1984; Lawler and Hero, 1997). Our experiments were designed to evaluate the potential impact of introduced trout on *A. canorus* by testing for palatability and antipredator behavior not only in larval stages of *A. canorus* found in lakes devoid of trout but also in larval life stages that co-occur with trout in the same water body.

MATERIALS AND METHODS

In June 2004, we collected newly oviposited eggs of *A. canorus* from Edith Lake, Inyo Co., California (37°33′19″N, 118°53′27″W), a lake containing *S. fontinalis*, and from a water body on Glacier Bench, Mono Co., CA (37°55′13″N, 119°14′15″W) devoid of trout. We refer to amphibians collected from waterbodies with *S. fontinalis* as "experi-

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Table 1. Summary of Palatability Experiments Using Different Lifestages of *A. canorus*.

Lifestage	Relationship with trout	Number of prey offered	Time trout starved (d)	Mean fork length ± S.E. of trout (mm)	Duration of experiment (h)	Number of replicates
egg	experienced	50	1.5	161.8 ± 2.5	8	5
egg	naïve	50	5	144.4 ± 2.7	8	5
tadpole	experienced	50	2	151.8 ± 3.0	24	5
tadpole	naïve	50	13	149.1 ± 5.5	24	5
postmetamorphic	experienced	40	4	162.1 ± 2.2	8	10
postmetamorphic	naïve	40	7	162.8 ± 3.7	8	10

enced'' and those collected from waterbodies without trout as ''naïve.'' Similarly *S. fontinalis* collected from water bodies without toads are called ''naïve.'' In August 2005, we collected postmetamorphic (young-of-the-year) naïve toads from Glacier Bench, experienced toads from Cloverleaf Lake (1 km upstream of Edith Lake), Inyo Co., CA (37°32′57″N, 118°53′44″W), which has *S. fontinalis*. Naïve tadpoles of *P. regilla* were also collected from Glacier Bench and a small fishless pond near Rock Creek Trailhead, Inyo Co., CA (37°25′17″N, 118°45′29″W). Naïve *S. fontinalis* (mean Fork Length 159.3 ± 2.0 mm S.E.) were collected by hook and line from Grass Lake, Inyo Co., CA (37°13′02″N, 118°37′47″W), a lake without *A. canorus* or adjacent (2 km) populations of toads. All animals were transported to the University of California, Santa Barbara, Sierra Nevada Aquatic Research Laboratory (SNARL) near Mammoth Lakes, California. All animals were maintained on a 14:10 h light:dark photoperiod for the duration of the experiments. Experiments were conducted 7 June–30 June 2004 and 25 August–1 September 2005. Trout were maintained in circular fiberglass holding tanks (120 cm diameter × 71 cm depth) that received a fresh inflow of stream water (Convict Creek) with a mean temperature of 15°C and were not fed for the duration of each experimental period. Eggs as well as tadpoles were held in aerated plastic dissecting pans (30 × 23 × 7 cm) and placed into a warm water immersion bath inside fish egg incubators (229 × 56 × 28 cm) with a mean temperature of 18°C. Toad eggs hatched in 4–5 days and developing tadpoles were fed a combination of ground rabbit chow and fish flake food *ad libitum*. Recently metamorphosed toads were held in 40 L glass aquaria with a dry artificial substrate and not fed prior to experiments. All lifestages were staged according to Gosner (1960) using a dissecting microscope, and individual toads as well as trout were only used once in experiments.

Palatability experiments.—We tested for palatability differences between experienced and naïve *A. canorus* as well as among eggs (stage 1–12), tadpoles (stage 23–25), and postmetamorphic (stage 46) toads with six ''no-choice'' experiments (Table 1). Toxicity of tadpoles has been shown to increase with development (Formanowicz and Brodie, 1982; Lawler and Hero, 1997; Crossland, 1998), suggesting that hatching and early stage tadpoles might be most vulnerable to predation. We therefore only used early stage (Gosner stage 23–25) tadpoles of *A. canorus* for our experiments.

Palatability experiments involving eggs and tadpoles consisted of ten naïve trout placed in separate, covered, 57 L aquaria (31 × 40 × 60 cm) that were filled with 40 L of stream water and partitioned with opaque dividers so that trout could not observe each other during experiments. Five trout were then randomly selected to receive ten single (separated from egg string) toad eggs or ten tadpoles. The remaining five trout acted as experimental controls for captive conditions and appetite testing post experiment. Palatability experiments for postmetamorphic toads consisted of 20 trout placed in aquaria as described above, of which ten were randomly selected to receive four postmetamorphic toads (mean snout–vent length 10.5 ± 0.2 mm S.E.) each. A small piece of floating material (5 × 5 cm) was placed in the center of the aquaria and anchored so that postmetamorphic toads had a place to rest in order to reduce the risk of drowning. The size of the refuge was designed so that all four toads could not rest simultaneously on the material. Furthermore, any toads found resting during observation recordings were displaced into the water. All trout were starved for a minimum of 1.5 d and as long as 13 d prior to experimentation. To minimize observer effects on timid trout, we did not continually observe or video record the experiments. Observations of remaining prey items in experiments were recorded every 0.5, 1, 2, 4, and 8 h for eggs and postmetamorphic toads, and every 0.5, 1, 2, 4, 8, 16, and 24 h for tadpoles. At the end of each 8 or 24 h experiment, willingness of trout to feed in captivity was assessed by offering control trout either an earthworm or tadpole of *P. regilla* for 1 h. Trout used in these experiments were not believed to be gape limited, as control trout readily consumed earthworms and tadpoles of *P. regilla* that were larger than tadpoles of *A. canorus* offered. Pairing equal numbers of control trout and trout offered toads was done to manage for potential toxic effects of consumption of toads in the event they were lethal to trout. Furthermore, this design also mitigated for other factors such as starvation and stress because trout were not fed while held in captivity nor was aquaria water exchanged during experiments. All experimental lifestages were monitored for 48 h post experiment.

Antipredator experiments.—We conducted three experiments to test if tadpoles of *A. canorus* responded to chemical cues of *S. fontinalis* through changes in activity levels. We hypothesized that even if toads were unpalatable they could still suffer lethal effects from being sampled by trout if they were unable to detect and subsequently respond to such threats. We theorized that larval life stages of *A. canorus* may not have the necessary chemical defenses to ward off trout predation, nor may they be able to respond behaviorally by avoiding detection due to the lack of a shared history with trout. Furthermore, if toads could not detect trout and were being depredated, then perhaps conspecific toads could warn other toads of this new predatory threat through chemical cues released into the water. We tested the ability of both naïve and experienced tadpoles of *A. canorus* to detect trout chemical cues. In addition, we tested the ability of tadpoles of *A. canorus* to detect trout chemical cues from trout fed a diet of tadpoles of *P. regilla*. Similar experiments using trout fed a diet of tadpoles of *A. canorus* were planned but not performed for reasons discussed in the Results section. For comparison with responses of *A. canorus*, we also tested the ability of tadpoles of *P. regilla*, a known palatable species, to detect trout chemical cues.

We used a gravitational flow-though system (Petranka et al., 1987) to pass water containing trout chemical cues into another container that contained eight toad tadpoles that we observed for behavioral responses to the cues. Three plastic 18 L containers (43 × 28 × 28 cm) were positioned at different heights and filled with untreated well water with a mean temperature of 15°C. The uppermost container served as a reservoir, while the middle container housed the stimulus (trout or no trout) and the lowermost container housed the tadpoles being observed. Containers were connected with aquarium airline tubing so that water flowed at a rate of 0.5–0.6 L/min. Trout and tadpoles were allowed to acclimate 30 min before flow was initiated. We measured behavior through activity level by the number of times tadpoles crossed a centerline in the container each minute for a 20 min period (Petranka et al., 1987). Each experiment was replicated ten times and consisted of two treatments. The first treatment consisted of one trout in a middle container to act as a predator chemical stimulus, and a second middle container treatment as a control (no trout) in which water flowed through an empty container. Trout were starved a minimum of 1.5 d to control for secondary alarm signal (e.g., ammonium) releases in effluent that could potentially influence tadpole behavior (Kiesecker et al., 1999).

We analyzed the activity responses using paired *t*-tests (SigmaStat, Chicago, IL, http://www.sigmaplot.com/products/SigmaStat/) with a two-tailed criterion because we were uncertain whether tadpoles would increase or decrease activity in response to chemical stimulus cues. A review of the literature regarding antipredator behavior in larval amphibians suggests both a decrease in activity (Lawler, 1989; Anholt et al., 1996) and an increase in activity (Hews and Blaustein, 1985).

Observation experiments.—Because it was observed that trout were willing to consume an earthworm or tadpoles of *P. regilla* at the end of the palatability experiments, we performed a series of observational experiments to examine if trout were able to differentiate between palatable and unpalatable prey items. First, we conducted ten 1 h experiments in which we offered tadpoles (stage 25) of *A. canorus* and *P. regilla* to trout. We placed a single trout in a glass aquaria (38 L) and then added tadpoles of each species in pairs every 2 min for the first 10 min of the trial. Injured or dead tadpoles were not removed during experiments, as trout were too timid in the presence of an observer. In the event a trout consumed all five tadpoles of *P. regilla* within the first ten minutes, an additional tadpole of *P. regilla* was added every 15 min to test if trout would continue to sample and differentiate between palatable and unpalatable prey. We recorded the number of times tadpoles were engulfed (i.e., taken into the mouth), rejected, or consumed.

We repeated the observational experiments with young-of-the-year postmetamorphic toads (stage 46) of *A. canorus* paired with tadpoles (stage 36–41) of *P. regilla*, as postmetamorphic stages of the latter species could climb out of aquaria. These experiments were shortened to 0.5 h so that postmetamorphic toads did not drown, as a resting platform was not provided. These experiments were video recorded to minimize observer effects. Only two prey items of each species were offered during these experiments, and subsequent prey items were not offered in order to not disturb trout behavior.

RESULTS

Palatability experiments.—Not a single egg, tadpole, or recently metamorphosed toad of *A. canorus* offered to trout were consumed in any of the palatability experiments. However, there was some evidence of sampling by trout. In one egg, one tadpole, and one postmetamorphic replicate, damage to individuals was observed. In the experiments with eggs, a total of six of 100 (6%) eggs of *A. canorus* had broken jelly coats or split embryos. All six damaged eggs were within a single trout container (i.e., replicate) in the experiment with naïve eggs, while the remaining eggs from the other four naïve-egg replicates as well as all eggs in the experiment with experienced eggs ($n = 50$) were undamaged. In the experiments with tadpoles, one out of 40 (2.5%) was semi-eviscerated, and was removed and replaced so that an equal number of mobile prey items were available for sampling by trout. This tadpole survived through 48 h post-experiment monitoring. In the experiments with postmetamorphic toads, one eviscerated toad was also removed, replaced, and in this case euthanized. This represented a total of 1 out of 80 (<1%) postmetamorphic toads offered to trout resulting in mortality. These data collectively suggest that at least a few trout actively sampled prey of *A. canorus* items offered but were not willing to consume them. The unwillingness of *S. fontinalis* to consume lifestages of *A. canorus* was not due to a lack of appetite under experimental conditions. In all six tadpole palatability experiments, control trout ($n = 40$) consumed a total of 27 of 40 (68%) earthworms offered. In experiments with postmetamorphic toads, control trout ($n = 20$) consumed 17 of 20 (85%) of *P. regilla* tadpoles offered.

Antipredator experiments.—There was no significant difference in activity levels between tadpoles of *A. canorus* exposed to trout chemical cues and controls for either experienced or naïve tadpoles (Table 2). We had initially intended to test the response of tadpoles of *A. canorus* to *S. fontinalis* that had been fed a diet of tadpoles of *A. canorus*; however, palatability experiments revealed that trout were not willing to accept larval stages of *A. canorus* as prey. As a surrogate, we decided to test the ability of tadpoles of *A. canorus* to respond to a nonconspecific threat using trout fed a diet of tadpoles of *P. regilla*. Again, we found no significant changes in activity levels (Table 2). In contrast to the results with toads, we found tadpoles of *P. regilla* significantly reduced activity when exposed to trout chemical cues (Table 2).

Observational experiments.—As with the palatability experiments, no tadpoles of *A. canorus* were consumed in any of the observational experiments. However, we were able to observe trout engulf or sample tadpoles repeatedly and do so without any apparent ill effect to the trout or toad. During tadpole experiments, 100% of tadpoles of *A. canorus*

Table 2. Response of Tadpoles of *A. canorus* and *P. regilla* to Chemical Cues of *S. fontinalis*. *P*-value is for a two-tailed paired t-test for differences in mean activity (number of crossing per minute) between trout stimulus and control (no trout) treatments. All treatments consisted of ten replicates.

Species	Relationship with trout	Predator stimulus	Mean crossing/minute		*P*-value
			Trout stimulus	Control	
A. canorus	experienced	*S. fontinalis*	1.25	1.37	0.735
A. canorus	naïve	*S. fontinalis*	3.00	3.82	0.186
A. canorus	naïve	*S. fontinalis* fed *P. regilla*	15.85	15.82	0.987
P. regilla	naïve	*S. fontinalis*	3.19	5.80	0.005

engulfed were rejected. In contrast, 80.6% of tadpoles of *P. regilla* that were engulfed were also consumed, while the remaining 19.4% engulfed were shortly rejected (Table 3). Furthermore, tadpoles of *P. regilla* that were engulfed and then rejected by trout ($n = 14$) were all eviscerated and ultimately died. By contrast, during one experiment, five tadpoles of *A. canorus* were engulfed and rejected 111 times unharmed. During two experiments, trout were active but unwilling to sample any tadpoles offered.

The results of observational experiments with postmetamorphic toads were remarkably different than those with toad tadpoles. On only two occasions did a trout actually engulf then reject a postmetamorphic toad, and each trout did so only once. In these two instances, postmetamorphic toads were rejected unharmed while trout appeared distressed and were observed shaking their heads with mouth agape. Tadpoles of *P. regilla* were also not as readily engulfed in these experiments as they were in the experiments with toads. Only four tadpoles out of 16 (25%) were consumed during these experiments. Trout activity was dramatically lower during these experiments, even in the absence of an observer, with trout usually remaining at the bottom of aquaria immobile for the first 10–15 min of the trial for reasons unknown.

DISCUSSION

Our research demonstrates that eggs, tadpoles, and recently metamorphosed toads of *A. canorus* are unpalatable to nonnative *S. fontinalis*, a species implicated in the decline of other native amphibians in the Sierra Nevada. Furthermore, we found no differences in palatability between naïve and experienced early lifestages of *A. canorus*. The fact that not a single egg, tadpole, or recently metamorphosed toad of *A. canorus* was consumed in any experiment is striking, especially because some trout were starved up to 312 h (13 d). *Anaxyrus canorus*, like most other bufonids, likely possess toxic properties throughout their aquatic and terrestrial life histories, rendering them unpalatable to trout. Flier et al. (1980) found that a class of cardiac glycosides (bufadienolides) in the skin may be responsible for unpalatable properties in toads. Intact ovarian eggs commonly found with depredated adult female *A. canorus* in the field suggest that these toxins may also be present in the eggs (R. Grasso, unpubl. data).

Our results are consistent with studies documenting the unpalatability of bufonid tadpoles to fish (Voris and Bacon, 1966; Kruse and Stone, 1984; Lawler and Hero, 1997) as well as to other vertebrates (Wassersug, 1971). There are a few fish species (Grubb, 1972; Kruse and Stone, 1984; Lawler and Hero, 1997) as well as some invertebrate predators (Formanowicz and Brodie, 1982) that will consume toad eggs or tadpoles as food items. Coincidentally, adult co-occurring *R. muscosa* have been observed eating tadpoles of *A. canorus* (Mullally, 1953), and a few other anurans will eat toad tadpoles (Bragg, 1940) as well as juvenile toads (Pearl and Hayes, 2002).

Although we suspect *S. fontinalis* are not negatively affecting populations of *A. canorus* through direct predation of eggs, tadpoles or postmetamorphic toads, sub-lethal effects from engulfing or sampling could potentially have an effect on development and survival rates of toads; however, our results suggest this is unlikely. A total of six (out of 100; 6%) damaged toad eggs, one (out of 40; 2.5%) eviscerated tadpole, and one (out of 80; <1%) eviscerated postmetamorphic toad were observed during palatability experiments as a result of sampling. The long duration of these experiments (8 to 24 h), use of starved trout, coupled with the fact that the "no-choice" design did not allow for alternate prey items, likely played a factor in the injury rates observed. Trout are unlikely to experience such conditions in the wild. Observational experiments demonstrated trout actively sampling prey items. Pacific Chorus Frogs were always preferred over toads in these observations. It was unclear during observational experiments whether trout

Table 3. Observational Experiments of *S. fontinalis* Offered Lifestages of *A. canorus* and *P. regilla* Together. The upper panel summarizes the results of ten separate experiments. In each experiment, one *S. fontinalis* was offered five tadpoles of *A. canorus* together with five to nine tadpoles of *P. regilla*. The lower panel summarizes six similar experiments using postmetamorphic toads. Percent rejected and percent consumed are based on the number of times a tadpole was engulfed.

Prey item	Number offered	Times engulfed	% Tadpoles rejected	% Tadpoles consumed
A. canorus	50	240	100	0
P. regilla	70	72	19.4	80.6
A. canorus (postmetamorphic)	12	2	100	0
P. regilla (tadpole)	12	4	0	100

were relying on visual or other olfactory clues when sampling tadpoles. It did not appear that trout could effectively differentiate between toads and chorus frogs using sight or smell, and thus apparently had to engulf tadpoles in order to assess palatability. When tadpoles were engulfed, trout would press the tadpole against the roof of the mouth before rejecting or consuming the tadpole. Tadpoles of *P. regilla* that were sampled then rejected in this manner were always eviscerated and rendered immobile, while tadpoles of *A. canorus* appeared unharmed and resumed activity almost immediately after rejection. Recent postmetamorphic toads that were repeatedly sampled (i.e., engulfed into the mouth and rejected) never exhibited any ill effects. During one observational trial, five tadpoles of *A. canorus* were engulfed and rejected over 111 times without any apparent harm.

Tadpoles of *A. canorus*, whether naïve or experienced, did not significantly change activity levels when exposed to water containing trout chemical cues. Tadpoles of many other species do respond to the presence of predator chemical cues (Petranka et al., 1987; Kats et al., 1988; Kiesecker et al., 1996). We found that naïve tadpoles of *P. regilla*, a palatable species, did significantly reduce their behavior when exposed to trout chemical cues. There are two potential reasons why tadpoles of *A. canorus* did not respond to chemical cues of trout. It is possible that tadpoles did in fact recognize trout presence through chemical cues but did not respond to such cues because they are unpalatable to trout and alterations in behavior are unnecessary and energetically costly. Alternatively, *A. canorus* may be unable to detect trout and are thus unable to respond to trout chemical cues.

Our palatability and observational experiments suggest that *A. canorus* is well protected from trout predation, and this may allow the two species to co-occur even though trout have been linked to the decline of other Sierra amphibians (Knapp et al., 2001; Matthews et al., 2001). Knapp (2005) found that *A. canorus* presence/absence was unrelated to trout presence. In the California Cascades, Welsh et al. (2006) found that the closely related Western Toad (*Anaxyrus boreas*) was positively associated with trout presence with toads being found four times more likely in lakes with trout versus lakes without trout. Trout may benefit populations of *A. canorus* through both a reduction in palatable amphibian competitors and native predators. For example, tadpoles and postmetamorphic toads of *A. canorus* have been observed in the field being consumed by adult as well as larval dytiscid beetles (Family Dytiscidae). Knapp et al. (2001) discovered that lakes with trout had significantly fewer dytiscid beetles present than lakes that were never stocked with trout, and trout stomach contents analyses confirmed both dytiscid beetle lifestages (R. Knapp, pers. comm., 2008). Since trout are not directly affecting populations of *A. canorus* in the same manner as other Sierra Nevada amphibians, removing trout from habitats occupied by *A. canorus* should not be a priority for managers. Investigations of other potential causes for decline of *A. canorus* is where future research should be focused.

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