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Growth and Behavioral Responses of Tadpoles of Two Native Frogs to an Exotic Competitor, *Rana catesbeiana*

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ABSTRACT.—*Rana catesbeiana* (American Bullfrog) is exotic in western North America and is sympatric with two native species, *Rana luteiventris* (Columbia Spotted Frog) and *Pseudacris regilla* (Pacific Treefrog). In a laboratory experiment, we assessed the growth of tadpoles of *R. luteiventris* and *P. regilla* in the presence and absence of tadpoles of *R. catesbeiana*. We found that in the presence of tadpoles of *R. catesbeiana*, *P. regilla* exhibited rapid growth in early larval stages compared to *R. luteiventris*. A second experiment indicated that, when reared with *R. catesbeiana*, *P. regilla* increased activity levels; this behavioral disparity may partly explain the observed difference in growth responses of the two frog species to *R. catesbeiana* competition. Our results suggest that tadpoles of *P. regilla* display greater growth and behavioral plasticity than do *R. luteiventris*, when subject to competition with *R. catesbeiana*. *Rana luteiventris* may be more susceptible than *P. regilla* to *R. catesbeiana*-mediated numerical decline, if exploitative or interference competition between tadpoles is a population-limiting factor in western breeding ponds.

Anuran community structure often depends on the outcome of larval competition, which is influenced by factors such as resource availability, larval growth rate, and predation (Wilbur, 1972; Wilbur et al., 1983; Relyea and Yurewicz, 2002; Garcia et al., 2004; Relyea, 2004). The effects of these factors on community structure are well studied among native species but are less understood when such assemblages include

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TABLE 1.   Repeated-measures ANOVA of tadpoles of *Rana luteiventris* versus *Pseudacris regilla* growth rates in the presence or absence of *Rana catesbeiana*.

	Mean square	df	F	P
Between				
Native species	23.422	1	78.298	<0.001
Rana catesbeiana presence	14.730	1	49.240	<0.001
Native × *Rana catesbeiana*	3.086	1	10.315	0.007
Error	0.299	12		
Within				
Growth (through time)	95.009	2	241.228	<0.001
Growth × species	31.439	2	79.822	<0.001
Growth × *Rana catesbeiana*	6.196	2	15.732	<0.001
Growth × species × *Rana catesbeiana*	3.358	2	8.526	0.002
Error	0.394	24		

exotic competitors. Understanding the effects of exotic competitors is important because biological invasions often lead to marked changes in population, community, and ecosystem processes (Hurlbert et al., 1972; Vitousek, 1990; Vitousek et al., 1996; Williamson, 1996).

Rana catesbeiana has undergone a rapid range expansion and numerical increase in the western United States, where it is an exotic species. Invasion by *R. catesbeiana* has coincided with reductions in the population size of several native ranid frog species. Despite widespread awareness of this correlation, the causal mechanism underlying these declines remains uncertain (Kiesecker et al., 2001). The hypothesis that western ranids have been reduced at breeding sites resulting from a combination of competition with, and predation by, *R. catesbeiana* (Moyle, 1973; Bury and Luckenbach, 1976; Hammerson, 1982; Clarkson and DeVos, 1986) has received recent empirical support for select anuran species (Kiesecker and Blaustein, 1997, 1998; Kupferberg, 1997; Kiesecker et al., 2001; Pearl et al., 2004). However, the response of native western species to *R. catesbeiana* can vary. Kupferberg (1997) found larval *R. catesbeiana* had greater negative effects on the growth and survivorship of larval *Rana boylii* than *Pseudacris regilla*. Although differential degrees of niche segregation with *R. catesbeiana* has been postulated as the source of such disparity in competitive response, the prevalence of this pattern among western anurans remains in question (Kupferberg, 1997).

Here we examine the effect of larval *R. catesbeiana* on larval growth rates in *Rana luteiventris* and *Pseudacris regilla*. Because *R. luteiventris* and *R. catesbeiana* are congeners and tadpoles of *Rana luteiventris* are considerably larger than those of *P. regilla*, exploitative or interference competition between *R. luteiventris* and *R. catesbeiana* may be more substantive (Werner, 1994; Kupferberg, 1997). Previous studies have found that, relative to *P. regilla*, ranid species exhibit poor larval growth in the presence of *R. catesbeiana* (Kiesecker and Blaustein, 1997; Kupferberg, 1997, 1998; Kiesecker et al., 2001). We predicted that tadpoles of *P. regilla* would compete better with tadpoles of *R. catesbeiana* by exhibiting higher per capita growth rates. Because such differences could be a result of heightened levels of

interference competition between *R. luteiventris* and *R. catesbeiana*, we also measured the effect of tadpoles of *R. catesbeiana* on *R. luteiventris* and *P. regilla* activity patterns in a separate experiment. Therein, we predicted that, when exposed to *R. catesbeiana*, *R. luteiventris* would exhibit lower activity levels than *P. regilla* (as in Kiesecker and Blaustein, 1997).

MATERIALS AND METHODS

We collected two *R. luteiventris* and 25 *P. regilla* egg masses from two ponds near Moscow, Idaho (46°50′N, 117°20′W). Egg masses were collected within 12 h of being deposited, and all egg masses were housed in species-specific outdoor aquaria containing ~ 25 liters of water. Tadpoles obtained from different egg masses were mixed homogeneously and housed indoors by species in 55-liter plastic tanks prior to use in the experimental trials.

Despite extensive surveys conducted during the two years preceding the experiments, *R. catesbeiana* were not observed in ponds used for *R. luteiventris* and *P. regilla* egg collection (Monello and Wright, 1999). We assumed that the tadpoles of *R. luteiventris* and *P. regilla* used in the present study were naïve to *R. catesbeiana* (see also Murray et al., 2004). We collected 80 tadpoles of *R. catesbeiana* that had over-wintered and were similar in size (3.3 ± 0.1 g, N = 20; mean mass ± SE) near Moscow. Tadpoles of *R. catesbeiana* were housed indoors in 55-liter plastic aquaria.

For tadpole maintenance in all experiments, ambient environmental conditions were kept at 20°C and on a 14 : 10 light : dark cycle. We replaced aquarium water on alternate days using aerated well water and provided tadpoles with pulverized commercial rabbit chow ad lib (in proportions that would not foul the water) until the start of each experiment. Tadpoles were randomly assigned to treatments.

Growth Experiment.—We used a two-factor repeated-measures design with four replicates to compare the growth of tadpoles of *R. luteiventris* and *P. regilla* in the presence or absence of tadpoles of *R. catesbeiana*. Ten tadpoles of *R. luteiventris* or *P. regilla* (three to five days old) were reared in the presence of zero or two tadpoles of *R. catesbeiana* in 15-liter plastic aquaria (34 × 18 × 24 cm). These densities are on the upper end of their natural range of variation for *P. regilla*
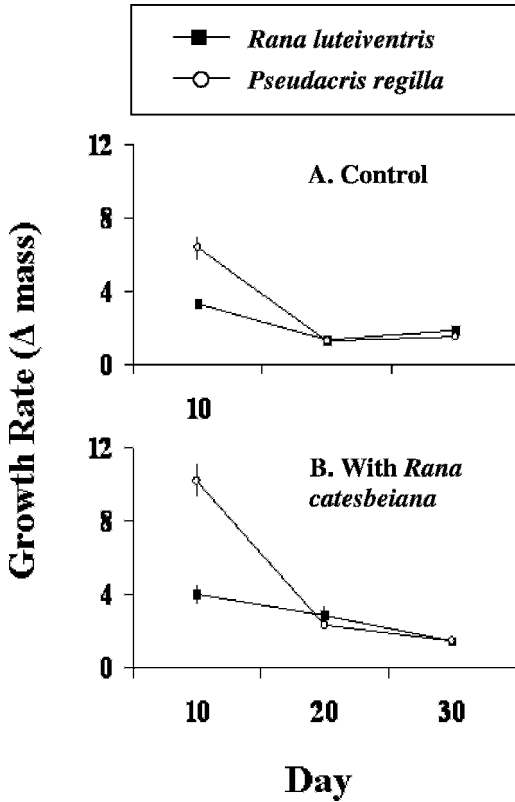
FIG. 1. *Rana luteiventris* and *Pseudacris regilla* tadpole growth rates (± SE) with (A) zero or (B) two *Rana catesbeiana* tadpoles per aquarium.

(Kupferberg, 1997). Control and experimental units received pulverized rabbit chow in rations of 3/20 of initial tadpole mass every other day (similar to Alford and Harris, 1988; Skelly and Werner, 1990).

Growth of tadpoles of *R. luteiventris* and *P. regilla* was measured every 10 days for 30 days. In an effort to maintain tadpole numbers over the course of each trial, we removed dead tadpoles ($N = 4$ throughout the course of the 30-day experiment) and replaced them with substitute tadpoles that had been reared under the same experimental conditions. The total mass of *R. catesbeiana* was measured at the start and

end of the experiment. Nonexperimental *R. luteiventris* and *P. regilla* ($N = 16$ for each species) were weighed at the outset of the experiment to calibrate growth curves and eliminate adverse handling effects on the recently hatched tadpoles used in the experiment. Conspecifics had similar weights prior to experimentation (*R. luteiventris* = 0.045 ± 0.001 g; *P. regilla* = 0.020 ± 0.001 g).

Activity Experiment.—We used a 2 × 2 factorial design replicated 20 times to measure the influence of *R. catesbeiana* tadpole exposure on the activity levels of preconditioned and naïve *R. luteiventris* and *P. regilla*. Tadpoles selected for preconditioning were maintained in 55-liter aquaria with 50 conspecifics and 10 *R. catesbeiana* for 10 days prior to the start of the experiment; naïve tadpoles were maintained under the same conditions but without *R. catesbeiana*. All subjects were fed ad libitum during the 10-day preconditioning interval, but no food was provided during the experiment itself.

Activity of individual, native tadpoles were measured in 5-liter aquaria (28 × 12 × 16 cm). Experimental treatments were stratified such that half of the animals within each test cohort (naïve *R. luteiventris*, preconditioned *R. luteiventris*, naïve *P. regilla*, preconditioned *P. regilla*) were subjected to the presence of a large tadpole of *R. catesbeiana*. For treatments with *R. catesbeiana*, we placed one tadpole of *R. catesbeiana* in the center of the aquarium and allowed it to acclimate for 10 min. Subsequently, a single tadpole of *R. luteiventris* or *P. regilla* (20–40 days old) was placed in the aquarium and allowed to acclimate for 10 min. We observed activity (moving or not moving) of *R. luteiventris* and *P. regilla* every 5 min for a total of 90 min.

Statistical Analysis.—*Rana luteiventris* are typically larger than *P. regilla*; thus, we considered changes in body mass ($mass_{t+1}/mass_t$), rather than absolute body mass, as metrics of competitive responses to tadpoles of *R. catesbeiana* among *R. luteiventris* and *P. regilla*. A value above 1.0 represents an increase in body mass. In the growth experiment, differences between species and experimental treatments were analyzed using repeated-measures ANOVA ($\alpha = 0.05$ for all statistical tests). We used a *t*-test to compare total *R. catesbeiana* mass in aquaria with *R. luteiventris* and *P. regilla* at the start and end of the experiment. For the activity experiment, we analyzed differences in *R. luteiventris* and *P. regilla* activity levels (% of observations with tadpoles moving) separately in the presence and

TABLE 2. ANOVAs of *Rana luteiventris* and *Pseudacris regilla* tadpole activity levels in the presence or absence of *Rana catesbeiana* tadpoles.

|	Mean square	df	F	P
(A) *Rana luteiventris* activity:				
Rana catesbeiana presence/absence	455.044	1	3.349	0.071
Preconditioned or not	77.533	1	0.571	0.452
Rana catesbeiana presence × preconditioned	22.276	1	0.164	0.687
(B) *Pseudacris regilla* activity:				
Rana catesbeiana presence/absence	127.856	1	1.169	0.283
Preconditioned or not	739.583	1	6.762	0.011
Rana catesbeiana presence x preconditioned	8.042	1	0.074	0.787
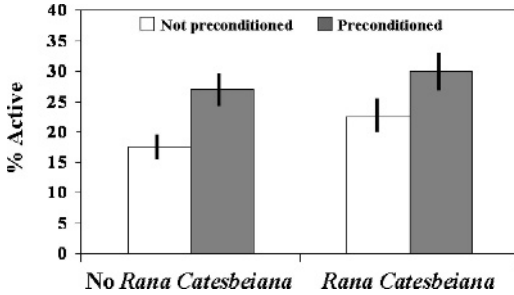
Fig. 2.   Proportion of observations (± SE) *Pseudacris regilla* tadpoles were active in the presence and absence of *Rana catesbeiana* tadpoles.

absence of *R. catesbeiana*. All percent data were arcsine square-root transformed (Krebs, 1989) and analyzed with ANOVA.

RESULTS

Growth Experiment.—The growth rate of tadpoles of *R. luteiventris* and *P. regilla* varied significantly over time (Table 1). Growth rates of both native species were high initially and then rapidly declined across all treatments (Fig. 1). Growth rates of tadpoles of *P. regilla* were significantly higher than those for *R. luteiventris*, but the interaction term between growth, *R. catesbeiana* presence, and native species was significant (Table 1, Fig. 1). The growth rate of tadpoles of *P. regilla* was more than twice that of *R. luteiventris* during the first 10 days of the experiment, but by day 20, there was little observable difference in growth rates between the species (Fig. 1). However, because of the higher initial growth rate of *P. regilla*, subsequent growth rates measures (e.g., measures taken on day 20 and day 30) indicate greater overall mass gain for tadpoles of *P. regilla* than *R. luteiventris*. For example, the overall growth rate (from day 0 to day 30) was twice as high for *P. regilla* (34.9 ± 2.7) than *R. luteiventris* (16.3 ± 1.7) in the presence of *R. catesbeiana*.

Total mass of *R. catesbeiana* did not differ among aquaria with *R. luteiventris* or *P. regilla* at the start (containers with *R. luteiventris* = 6.5 ± 0.11 g, *P. regilla* = 6.4 ± 0.10 g; $t_6 = 0.49$, $P = 0.64$) or end of the experiment (containers with *R. luteiventris* = 9.6 ± 0.65 g, *P. regilla* = 8.6 ± 0.90 g; $t_6 = 0.65$, $P = 0.54$).

Activity Experiment.—Activity of tadpoles of *R. luteiventris* did not differ among treatments or tadpoles subject to *R. catesbeiana* preconditioning (Table 2). *Pseudacris regilla* did not vary their activity patterns in the presence of *R. catesbeiana* (Table 2). However, *P. regilla* that were preconditioned to *R. catesbeiana* had higher activity levels (0.29 ± 0.02; % of observations with tadpoles moving) than those that were not preconditioned (0.20 ± 0.02; $P = 0.011$, Fig. 2).

DISCUSSION

The results of this investigation provide support for the hypothesis that tadpoles of *P. regilla* are better able to respond to the presence of tadpoles of *R. catesbeiana* than are tadpoles of *R. luteiventris*. *Pseudacris regilla* exhibited significantly higher growth rates in the presence of *R. catesbeiana* and had per capita growth rates that were twice as great as *R. luteiventris* in the

experimental and control treatments. The disparity between the growth rates of the two test species was greatest during the first 10 days of larval development. *Rana luteiventris* showed no response to the presence of *R. catesbeiana*.

Rapid growth during the larval stage has been linked to enhanced competitive ability in several amphibians (Werner, 1992; Wells and Harris, 2001). Increased rates of larval growth in anurans also have been associated with reduced vulnerability to predation (Brodie and Formanowicz, 1983; Semlitsch and Gibbons, 1988; Semlitsch, 1990). For example, in gaining size rapidly, larvae may become stronger and more vigorous, and consequently more difficult for predators to capture and subdue (Formanowicz, 1986). In light of the numerous fitness benefits associated with rapid size gain, we expect larval anurans to capitalize on food availability by manifesting increased initial growth rates. In this study, *P. regilla* growth rates were consistent with this prediction. By contrast, *R. luteiventris* tadpole growth was similar in the presence and absence of *R. catesbeiana*, implying that *P. regilla* increased their activity and feeding levels (e.g., Werner, 1992).

The results of the activity experiment suggest that the physiological disparity in the responses of tadpoles of *R. luteiventris* and *P. regilla* to the presence of *R. catesbeiana* may have been mediated by behavior. Preconditioned *P. regilla* were significantly more active in the presence and absence of *R. catesbeiana* than were naïve conspecifics that had not been raised with *R. catesbeiana*. Activity levels of *R. luteiventris* did not differ between treatments. The link between increased activity levels, resource acquisition, and heightened larval growth is well established (Werner and Anholt, 1993). Werner (1992) found *Rana pipiens* (Leopard Frog) manifested higher larval growth rates than *Rana sylvatica* (Wood Frog) resulting from heightened activity levels, which in turn led to competitive superiority in the former species. Similarly, Wells and Harris (2001) argue that higher growth rates among *Ambystoma jeffersonianum* (Jefferson Salamander) versus *Hemidactylium scutatum* (Four-Toed Salamander) were a result of increased activity in the former species. We cannot rule out the possibility that that the activity levels of preconditioned *P. regilla* were a response to being raised in aquaria with greater densities of tadpoles. However, our results are consistent with previous work that suggests the increased activity levels displayed by *P. regilla* enabled them to increase their growth rates.

Our results shed light on the relevance of *R. catesbeiana* competition in anuran communities of the western United States. Adverse behavioral (and in turn growth) responses to an invasive competitor may reduce individual productivity, survival, and ultimately, species persistence. Hence, efforts to conserve anurans that may be influenced by expansion of the *R. catesbeiana* in the western United States should perhaps selectively focus on congeners with high levels of niche overlap, relatively large tadpoles, and relatively slow larval growth rates. Anuran species whose biological characteristics resemble those of *P. regilla* should be less adversely affected by the presence of *R. catesbeiana* and, therefore, may be less likely to face local extirpation. However, it is

important to note that, given the controlled nature of our laboratory experiment, the applicability of our findings to field situations remain in question. Therefore, future studies need to focus on testing our predictions through field experiments where *R. catesbeiana* impacts on native frog species can be assessed in more natural contexts.

LITERATURE CITED

ALFORD, R. A., AND R. N. HARRIS. 1988. Effects of larval growth history on anuran metamorphosis. American Naturalist 131:91–106.

BRODIE JR., E. D., AND D. FORMANOWICZ JR. 1983. Prey size preference of predators: differential vulnerability of larval anurans. Herpetologica 39:67–75.

BURY, R. B., AND R. A. LUCKENBACH. 1976. Introduced amphibians and reptiles in California. Biological Conservation 10:1–14.

CLARKSON, R. W., AND J. S. DEVOS JR. 1986. The bullfrog, *R. catesbeiana* Shaw, in the lower Colorado River, Arizona, California. Journal of Herpetology 20: 42–49.

FORMANOWICZ JR., D. R. 1986. Anuran tadpole/aquatic insect predator-prey interactions: tadpole size and predator capture success. Herpetologica 42:367–373.

GARCIA, T. S., J. STACY, AND A. SIH. 2004. Larval salamander response to UV radiation and predation risk: color change and microhabitat use. Ecological Applications 14:1055–1064.

HAMMERSON, G. A. 1982. Bullfrog eliminating Leopard Frogs in Colorado? Herpetological Review 13: 115–116.

HURLBERT, S. H., J. ZEDLER, AND D. FAIRBANKS. 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. Science 175:639–641.

KIESECKER, J. M., AND A. R. BLAUSTEIN. 1997. Population differences in responses of Red-Legged Frogs (*Rana aurora*) to introduced bullfrogs. Ecology 78:1752–1760.

———. 1998. Effects of introduced bullfrogs and smallmouth bass on microhabitat use, growth, and survival of native Red-Legged Frogs (*Rana aurora*). Conservation Biology 12:776–787.

KIESECKER, J. M., A. R. BLAUSTEIN, AND C. L. MILLER. 2001. Potential mechanisms underlying the displacement of native Red-Legged Frogs by introduced bullfrogs. Ecology 82:1964–1970.

KREBS, C. J. 1989. Ecological Methodology. Harper Collins Publishers, New York.

KUPFERBERG, S. J. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. Ecology 78:1736–1751.

MONELLO, R. J., AND R. G. WRIGHT. 1999. Amphibian habitat preferences among artificial ponds in the Palouse region of northern Idaho. Journal of Herpetology 33:298–303.

MOYLE, P. B. 1973. Effects of introduced bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. Copeia 1973:18–22.

MURRAY, D. L., J. D. ROTH, AND A. J. WIRSING. 2004. Predation risk avoidance by terrestrial amphibians: the role of prey experience and vulnerability to native and exotic predators. Ethology 110: 635–647.

PEARL, C. A., M. J. ADAMS, R. B. BURY, AND B. MCCREARY. 2004. Asymmetrical effects of introduced bullfrogs (*Rana catesbeiana*) on native ranid frogs in Oregon. Copeia 2004:11–20.

RELYEA, R. A. 2004. Fine-tuned phenotypes: tadpole plasticity under 16 combinations of predators and competitors. Ecology 85:172–179.

RELYEA, R. A., AND K. L. YUREWICZ. 2002. Predicting community outcomes from pairwise interactions: integrating density- and trait-mediated effects. Oecologia 131:569–579.

SEMLITSCH, R. D. 1990. Effects of body size, sibship and tail injury on the susceptibility of tadpoles to dragonfly predation. Canadian Journal of Zoology 68:1027–1030.

SEMLITSCH, R. D., AND J. W. GIBBONS. 1988. Fish predation in size-structured populations of treefrog tadpoles. Oecologia 75:321–326.

SKELLY, D. K., AND E. E. WERNER. 1990. Behavioral and life-historical responses of larval American toads to an odonate predator. Ecology 71:2313–2322.

VITOUSEK, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57: 7–13.

VITOUSEK, P. M., C. M. D'ANTONIO, L. L. LOOPE, AND R. WESTBROOKS. 1996. Biological invasions as global environmental change. American Scientist 84: 468–478.

WELLS, C. S., AND R. N. HARRIS. 2001. Activity level and the tradeoff between growth and survival in the salamanders *Ambystoma jeffersonianum* and *Hemidactlyium scutatum*. Herpetologica 57:116–127.

WERNER, E. E. 1992. Competitive interactions between wood frog and northern leopard frog larvae: the influence of size and activity. Copeia 1992:26–35.

———. 1994. Ontogenetic scaling of competitive relations—size-dependent effects and responses in two anuran larvae. Ecology 75:197–213.

WERNER, E. E., AND B. R. ANHOLT. 1993. Ecological consequences of the tradeoff between growth and mortality rates mediated by foraging activity. American Naturalist 142:242–272.

WILBUR, H. M. 1972. Competition, predation, and the structure of the *Ambystoma-Rana sylvatica* community. Ecology 53:3–21.

WILBUR, H. M., P. J. MORIN, AND R. N. HARRIS. 1983. Salamander predation and the structure of experimental communities: Anuran responses. Ecology 64:1423–1429.

WILLIAMSON, R. 1996. Biological Invasions. Chapman and Hall, London.