Effects of Introduced Bullfrogs and Smallmouth Bass on Microhabitat Use, Growth, and Survival of Native Red-Legged Frogs (*Rana aurora*)

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Abstract: *We examined the direct and indirect effects of two introduced species, the bullfrog (*Rana catesbeiana*) and smallmouth bass (*Micropterus dolomieui*), on the microhabitat use, growth, development, and survival of larval and metamorphic red-legged frogs (*Rana aurora*). In field enclosure experiments, tadpoles of* R. aurora *altered their microhabitat use in the presence of both species. The shift in microhabitat use by* R. aurora *corresponded to increased activity in adult* R. catesbeiana. *Time to metamorphosis increased and mass at metamorphosis decreased when* R. aurora *tadpoles were exposed to either larval or adult* R. catesbeiana. *In contrast, smallmouth bass alone had little effect on the growth and development of* R. aurora. *In all experiments, survivorship of* R. aurora *was significantly affected only when* R. aurora *were exposed to the combined effects of bullfrog larvae and adults or bullfrog larvae and smallmouth bass. Thus, the interaction between stages (larval-adult) or species (bullfrog–smallmouth bass) produced indirect effects that were greater than when each factor was considered separately.*

Efectos de la Introducción de la Rana toro *Rana catesbeiana* y el Pez *Micropterus dolomieui* en el Uso del Microhabitat, Crecimiento y Supervivencia de la Rana patiroja *Rana aurora*

Resumen: *Examinamos los efectos directos e indirectos de dos especies introducidas; la rana toro* Rana catesbeiana *y el pez* Micropterus dolomieui *en el uso del microhabitat, crecimiento, desarrollo y supervivencia de la Rana patiroja* Rana aurora *en estados larvales y metamórficos. En encierros experimentales de campo, los renacuajos de* R. aurora *alteraron el uso de su microhábitat en presencia de ambas especies. El cambio en uso de microhábitat por* R. aurora *correspondió con un incremento en la actividad de adultos de* R. catesbeiana. *El tiempo de metamorfósis incrementó y la masa durante metamorfósis disminuyó cuando los renacuajos de* R. aurora *fueron expuestos tanto a larvas como adultos de* R. catesbeiana. *En contraste, la presencia de solo* Micropterus dolomieui *tuvo poco efecto en el crecimiento y desarrollo de* R. aurora. *En todos los experimentos la supervivencia de* R. aurora *fue significativamente afectada solo cuando* R. aurora *estuvo expuesta a los efectos combinados de larvas y adultos de la rana toro y el pez. Por lo tanto, la interacción entre estados (larval/adulto) o especies (*rana toro*/Micropterus) produjo efectos indirectos que fueron mayores que cuando cada factor se consideró por separado.*

Paper submitted March 17, 1997; revised manuscript accepted October 30, 1997.

Introduction

The introduction and spread of exotic species is a global phenomenon (Elton 1958) that poses critical problems for many natural ecosystems (Drake et al. 1989; Krebs 1994). The mechanisms that enable exotic species to thrive at the expense of native species are often unclear (Lodge 1993). Although there are many examples of native species declining after the arrival of an exotic species (see reviews in Elton 1958; Lodge 1993; Krebs 1994), the mechanism underlying the decline is often unknown. Competition or predation is frequently proposed to explain population declines or habitat shifts of native species after exotic introductions, but such mechanisms are rarely isolated and tested in an experimental setting. The importance of understanding the mechanisms that allow exotic species to thrive, often at the expense of native species, takes on new urgency as invasions of alien species alter ecosystems (Vitousek 1989, 1990; Lodge 1993), modify trophic structure (Wormington & Leach 1992; Holland 1993; Nicholls & Hopkins 1993), and displace species (Zaret & Paine 1973; Groves & Burdon 1986; Savidge 1988; Haag et al. 1993; Petren et al. 1993; Gamradt & Kats 1996; Petren & Case 1996; Gamradt et al. 1997; Kupferberg 1997).

Understanding the mechanisms that facilitate the success of exotic species can be particularly difficult when interactions between native and exotic species involve more than a single developmental stage. Thus, the overall dynamic between the two species may comprise a web of interactions containing both direct and indirect effects. For example, many organisms exhibit marked niche shifts and trophic level changes throughout their ontogeny. These ontogenetic shifts may influence interactions between species (Werner & Gilliam 1984; Stein et al. 1988; Olson et al. 1995). This may be especially true for many anuran amphibians that undergo a shift from herbivorous larvae to carnivorous adults (Duellmann & Trueb 1986). Thus, to fully understand the overall impact of introduced species on native species, experimental tests should include the various life stages of an exotic organism which may influence natives.

We present experimental evidence suggesting that introduced bullfrogs (*Rana catesbeiana*) in combination with smallmouth bass (*Micropterus dolomieui*) have negative effects on native red-legged frogs (*Rana aurora*), influencing their microhabitat use, growth, and development. Several studies have documented the decline of native ranid frogs after the introduction of bullfrogs and predatory fish (Moyle 1973; Bury & Luckenbach 1976; Green 1978; Hammerson 1982; Clarkson & DeVos 1986; Fisher & Shaffer 1996). These studies, however, only suggest a negative association between introduced species and native frogs. Few studies have attempted to examine experimentally the mechanism by which introduced organisms affect ranid frogs (but see Kupferberg 1997).

Natural History

Rana aurora occur west of the Cascade–Sierra Nevada Mountains from British Columbia, Canada, to northern Baja California, U.S.A. (Stebbins 1985). Breeding habitats vary from small, ephemeral ponds to large lakes. In Oregon *R. aurora* breed from December to March, and larvae reach metamorphosis in 2–3 months (Nussbaum et al. 1983). After breeding, adult red-legged frogs are highly terrestrial and can be found far from aquatic habitats (Nussbaum et al. 1983, personal observation). Like some other species (e.g., Crump et al. 1992; Richards et al. 1993; Blaustein et al. 1994*a*; Pounds et al. 1997), *R. aurora* has exhibited marked range contractions and population declines (Nussbaum et al. 1983; Stebbins & Cohen 1995; Fisher & Shaffer 1996). In fact, the California subspecies (*R. aurora draytonii*) has recently been listed as threatened by the U.S. Fish and Wildlife Service (Federal Register 1996).

Interactions with introduced bullfrogs are continually invoked as a primary cause for losses of red-legged frogs (Moyle 1973; Bury & Luckenbach 1976; Bury et al. 1980; Nussbaum et al. 1983; Hayes & Jennings 1986; Blaustein 1994). *Rana catesbeiana* is native to the eastern United States, occurring naturally as far west as the great plains (Nussbaum et al. 1983; Stebbins 1985). Bullfrogs, however, have been extensively introduced throughout much of the western United States, including much of Oregon west of the Cascade mountains (Nussbaum et al. 1983; Hayes & Jennings 1986; Stebbins & Cohen 1995).

Adult bullfrogs feed on a variety of aquatic prey, including other amphibians (Corse & Metter 1980; Bury & Whelan 1986; Beringer & Johnson 1995; Werner et al. 1995). Both tadpoles and adults of *R. catesbeiana* prey on tadpoles of other species (Ehrlich 1979; Bury & Whelan 1986; Werner et al. 1995; Kiesecker & Blaustein 1997*b*). In Oregon, bullfrogs typically breed from June to August, and larval bullfrogs take 1–3 years to reach metamorphosis (Nussbaum et al. 1983). Thus, the larvae of native species of frogs such as *R. aurora* may be exposed to larger, older bullfrog tadpoles.

The introduction of several species of nonnative predatory fish, including smallmouth bass (*Micropterus dolomieui*), may also contribute to population declines of ranid frogs (Hayes & Jennings 1986). Smallmouth bass are known to prey on larval amphibians, including red-legged frog larvae (Scott & Crossman 1973; Kruse & Francis 1977; J. M. K., personal observation). Historically, smallmouth bass were restricted to central and eastern North America, but they have since been introduced throughout western North America (Lee et al. 1980; Minckley & Deacon 1991). Predation by nonnative fish can have negative effects on native frog populations (Bradford 1989; Bradford et al. 1993). Furthermore, exotic fish may exert indirect effects by introducing pathogens that can be transmitted to amphibians (Blaustein et al. 1994*b*; Kiesecker & Blaustein 1995, 1997*a*).

The specific impacts of bullfrogs or fish on native frog populations is often unclear because at many sites their introductions have occurred simultaneously. Also, the impact that one introduced species has may be influenced by the presence of other exotic species. For example, *R. aurora* larvae are known to alter their behavior in the presence of bullfrog adults and larvae (Kiesecker & Blaustein 1997*b*). Changes in behavior in the presence of bullfrogs may make *R. aurora* larvae more susceptible to predatory fish. Also, changes in behavior may influence microhabitat use, which may in turn influence growth and development.

Methods

Collection and Maintenance

All red-legged frog larvae used in experiments were collected as embryos (20 clutches; 12 in 1994, 8 in 1995) from a marsh where both bullfrogs and smallmouth bass currently occur (12 miles south of Springfield, Lane County, Oregon, U.S.A.) and transported to our laboratory in Corvallis, Oregon. Bullfrog adults and tadpoles used in experiments were collected from the north marsh on the E. E. Wilson Wildlife Refuge (18 km north of Corvallis, Benton County, Oregon). Field studies took place at the south marsh on the E. E. Wilson Wildlife Area.

We kept *R. aurora* eggs in aerated, 38-L aquaria filled with dechlorinated tap water. After hatching, tadpoles were transported to field enclosures for use in the bullfrog field enclosure experiment and the bullfrog–smallmouth bass field enclosure experiment. Approximately 600 tadpoles remained in the laboratory until metamorphosis, after which they were transported to field enclosures for use in the bullfrog–red-legged frog metamorph experiment.

EFFECTS OF BULLFROGS ON RED-LEGGED FROG LARVAE (EXPERIMENT 1)

We assessed the impact of larval and adult bullfrogs on the habitat use, growth, development, and survival of *R. aurora* in experiments at the south marsh of the E. E. Wilson Wildlife Refuge. We used rectangular, open-bottom pens (8 × 4 m, 32 m^2) constructed of 1-mm^2 mesh fiberglass screen that was pressed approximately 20 cm into the soft mud substrate. Each enclosure was placed perpendicular to the shore line. Water depth ranged from approximately 10 cm near the shore to approximately 1.5 m away from the shore. Before tadpoles were added, enclosures were cleared of their macrofauna (e.g., corixids, notonectids) by repeated sweeping with a net. After tadpoles were added, invertebrates were allowed to colonize the enclosures naturally. Other than the experimental animals, no vertebrates were observed in the enclosures. To minimize potential spatial gradients (e.g., temperature, vegetation) from confounding treatment effects, enclosures were blocked and treatments were assigned randomly within blocks.

We used a fully factorial design with all combinations of the presence and absence of larval and adult bullfrogs. Four treatments, each replicated three times for a total of 12 enclosures, were adult bullfrog only (1 bullfrog adult, 150 *R. aurora* larvae), larval bullfrogs only (50 bullfrog larvae, 100 *R. aurora* larvae), adult and larval bullfrogs (1 bullfrog adult, 50 bullfrog larvae, 100 *R. aurora* larvae), and no bullfrogs (150 *R. aurora* larvae). We controlled for overall density of larvae (150) to ensure that the negative effects of *R. catesbeiana* larvae on *R. aurora* were due to interspecific effects and not increased density. Densities of both species were comparable to densities observed at other field sites (J. Kiesecker, unpublished data). All hatchling *R. aurora* larvae (0.01 ± 0.001 g, mean ± 1 SE; Gosner stage 25 [Gosner 1960]; $n = 100$) were matched for developmental stage and size, as were first-year *R. catesbeiana* larvae (7.8 ± 1.1 g, mean ± 1 SE; Gosner stage 25 [Gosner 1960]; $n = 300$). *Rana catesbeiana* adults were also matched for size (114.7 ± 13.1 g, mean ± 1 SE; $n = 6$).

To reflect the natural breeding phenology in ponds where the two species are found, *R. catesbeiana* adults and larvae were present in the enclosures prior to the addition of *R. aurora* larvae (Nussbaum et al. 1983). Adult and larval *R. catesbeiana* were added to enclosures on 27 October 1993 and 16 January 1994, respectively. Hatchling *R. aurora* were added on 30 January 1994.

Once every seventh day the position of tadpoles within the enclosures was determined by using funnel traps placed 2, 4, and 6 m from the shore line. Traps were placed in enclosures for 24 hours, and we identified the species and counted the number of tadpoles captured at each trap. We consistently captured 80% or more of the tadpoles in each enclosure during sampling. Traps measured 72 × 55 × 20 cm, with mouth and apical openings of 15 and 5 cm in diameter, and were constructed of fiberglass screen and wire. In each enclosure the average position of tadpoles of each species was estimated by ranking the number of tadpoles at each distance and dividing this by the total number of tadpoles caught in the traps, giving the average ranked tadpole position. Water temperature was measured with a Barnant 115 thermocoupler three times a day (0600, 1200, and 1800 hours) at each trap at a depth of 50 cm. Adult bullfrog activity was assessed with daily visual surveys. Adults were considered "active" when they could be seen moving in the enclosures.

We terminated the experiment when all *R. aurora* had either metamorphosed or died. Our criterion for metamorphosis was front limb emergence (Gosner stage 42; Gosner 1960). We checked for metamorphs daily. Individuals were removed from the enclosures as they metamorphosed, and mass (to the nearest mg) and time (in days) at metamorphosis were recorded.

EFFECTS OF BULLFROGS ON METAMORPHOSED RED-LEGGED FROGS (EXPERIMENT 2)

We assessed the impact of the presence of adult *R. catesbeiana* on the survival of *R. aurora* metamorphs (Gosner stage 44). Enclosures used in this experiment were identical to those used in experiment 1, except that half of each enclosure was in water and half was on land. The depth of water in the deep end of each enclosure was approximately 1.0 m. This allowed metamorphs of *R. aurora* to complete metamorphosis and move onto land. A line of pitfall traps (4 m long, 20 cm wide) were placed on the terrestrial portion of the enclosures 2 m from the shoreline. This ensured that any of the metamorphs would be captured as they moved onto land. Enclosures were blocked and treatments were assigned randomly within blocks.

In 6 of the enclosures, a single adult *R. catesbeiana* was added on 20 March 1994. On 27 March 1994, 50 *R. aurora* metamorphs were added to all 12 enclosures. Metamorphs were animals raised in our lab for this experiment. Densities of both species were comparable to densities observed at other field sites (J. Kiesecker, unpublished data). All *R. aurora* (1.11 ± 0.41 g, mean ± 1 SE; Gosner stage 44, [Gosner 1960]; $n = 600$) metamorphs were matched for developmental stage and size. *Rana catesbeiana* adults were also matched for size (124.3 ± 17.1 g, mean ± 1 SE; $n = 6$).

The experiment was terminated when all *R. aurora* had either metamorphosed or died. We removed individuals from the pitfall traps each day and recorded the number surviving in each enclosure. Funnels over the top of the pitfall traps prevented bullfrog adults from eating *R. aurora* once they were inside the traps.

EFFECTS OF BULLFROGS AND BASS ON RED-LEGGED FROG LARVAE (EXPERIMENT 3)

We conducted a field experiment to evaluate the combined effects of larval bullfrogs and introduced fish on *R. aurora* habitat use, growth, development, and survival. Enclosures and procedures used in this experiment were identical to those used in experiment 1.

In a fully factorial design, all combinations of the presence or absence of smallmouth bass and larval bullfrogs were crossed. The resulting four treatments were each replicated three times for a total of 12 enclosures. Smallmouth bass and *R. catesbeiana* larvae were both added to enclosures on 1 February 1995, whereas *R. aurora* larvae were added on 15 February 1995.

Densities of both species were comparable to densities observed at other field sites (J. Kiesecker, unpublished data). All hatchling *R. aurora* (0.02 ± 0.004 g, mean ± 1 SE; Gosner stage 25 [Gosner 1960]; $n = 100$) larvae were matched for developmental stage and size, as were first year *R. catesbeiana* larvae (6.9 ± 1.1 g, mean ± 1 SE; Gosner stage 25 [Gosner 1960]; $n = 300$). *Micropterus dolomieui* were also matched for total length (113.7 ± 10.1 mm, mean ± 1 SE; $n = 6$).

Statistical Analyses

Multivariate analysis of variance (MANOVA) was used to test for differences in the effect of independent factors (larval bullfrogs and adult bullfrog in experiment 1, and larval bullfrogs and smallmouth bass in experiment 3) on the dependent variables of time (mean days to metamorphosis), mass (mean mass at metamorphosis), and survivorship (mean survivorship to metamorphosis) (Tabachnick & Fidell 1989). After MANOVA we used Bonferroni adjusted univariate analysis of variance (ANOVA) on each response variable to assess which variables were responsible for significant main effects. Post hoc comparisons (Tukey Test) were performed to test for differences between means among the treatments (Zar 1984). For experiments 1 and 3 we also tested for differences in microhabitat use by *R. aurora* by using a two-way repeated measures ANOVA. We used the average ranked tadpole position of each enclosure from each sampling period in statistical tests. For experiment 2 we tested for differences in survival between treatments with a Student's *t* test.

For all experiments, a preliminary analysis indicated no significant block effects. Therefore, the block and error terms were pooled for remaining tests (Zar 1984). Because individuals in enclosures were not independent of one another, these measures were analyzed as enclosure means. For all experiments, parametric assumptions were met and no data transformations were necessary.

Results

Experiment 1

The presence of *R. catesbeiana* adults and tadpoles significantly interacted to effect *R. aurora* growth, development, and survivorship (Table 1). We interpreted these effects for each response variable by means of the univariate tests and post hoc comparison (Tukey tests).

Exposure to both adult and larval bullfrogs influenced *R. aurora* mass at metamorphosis (Table 1; Fig. 1). Mass was greatest for *R. aurora* when alone than in any of the other treatments (Tukey HSD $p < 0.001$; Fig. 2). Red-

Table 1. Results of MANOVA for overall effects of *Rana catesbeiana* adult and tadpoles on *Rana aurora* survival, growth, and time to metamorphosis, and ANOVAs for each response variable.

	F	*df*	p
MANOVA			
constant	5827.785	3, 6	<0.001
adult	95.357	3, 6	<0.001
larvae	43.594	3, 6	<0.001
adult × larvae	15.023	3, 6	0.003
ANOVAs*			
Mass			
adult	79.852	1, 8	<0.001
larvae	20.136	1, 8	0.002
adult × larvae	2.767	1, 8	0.135
Time			
adult	66.057	1, 8	<0.001
larvae	30.229	1, 8	0.001
adult × larvae	0.914	1, 8	0.367
Survival			
adult	51.682	1, 8	<0.001
larvae	49.960	1, 8	<0.001
adult × larvae	49.723	1, 8	<0.001

**Response variables are proportion surviving (survival), mass at metamorphosis (mass), and time to metamorphosis (time). Significance level for univariate tests is 0.0125 (Bonferroni-adjusted for three response variables).*

legged frogs with only adult bullfrogs had a higher mass than red-legged frogs with both adult and larval bullfrogs (Tukey HSD $p = 0.02$). Mass at metamorphosis for *R. aurora* exposed only to larval bullfrogs did not differ from mass in the combined treatment (Tukey HSD $p < 0.098$; Table 1), suggesting that larval bullfrogs had the stronger effect on red-legged frogs mass.

Both adult and larval bullfrogs increased the time to metamorphosis of red-legged frogs (Table 1; Fig. 1). Time to metamorphosis was fastest for *R. aurora* when alone than in any of the other treatments (Tukey HSD $p < 0.01$; Fig. 1). There was no difference in time to metamorphosis between *R. aurora* exposed to either adult or larval bullfrogs only (Tukey HSD $p = 0.67$), suggesting that adult and larval bullfrogs had similar effects on the developmental time of *R. aurora*.

The combined effects of both adult and larval bullfrogs influenced survival to metamorphosis of *R. aurora* (Table 1; Fig. 1). Survivorship was generally high for *R. aurora* when alone or either with bullfrog tadpoles only or bullfrog adults only, averaging 84.3%, 86.1%, and 82.3%, respectively. The survivorship of *R. aurora*, however, was decreased to 69.3% (Tukey HSD $p < 0.01$) in the presence of both larval and adult bullfrogs. Survivorship for adult and larval bullfrogs was 100% and 94.7%, respectively.

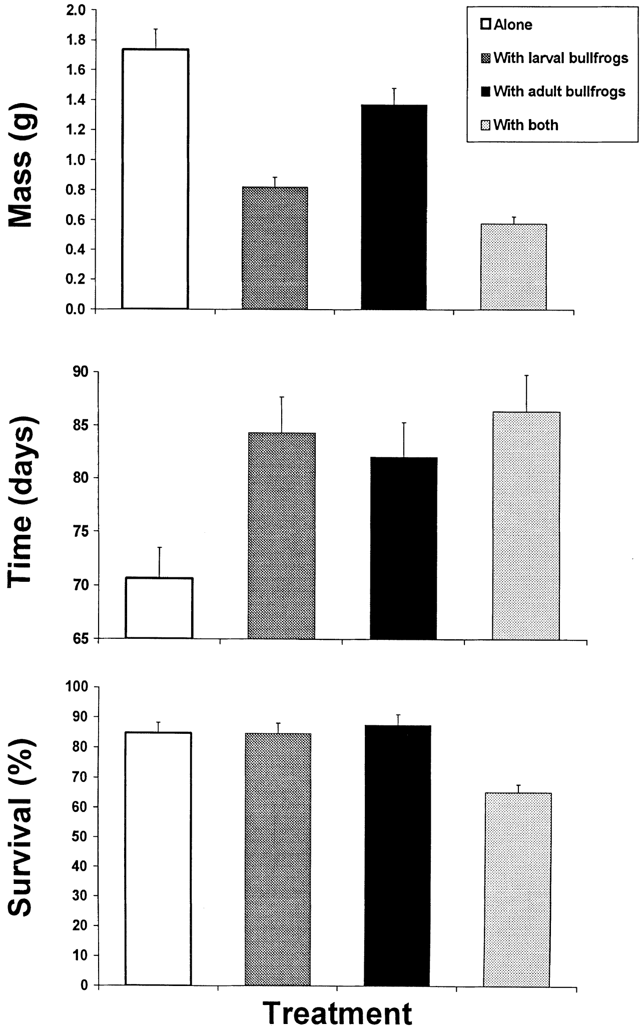

Figure 1. Mean (± 1 SE) mass at, time to, and survival to metamorphosis for Rana aurora *larvae exposed to larval and adult bullfrogs (*Rana catesbeiana*) in field enclosures.*

Microhabitat use by larval *R. aurora* changed during the experiment and was significantly altered by the presence of adult and larval bullfrogs (Table 2). When *R. aurora* larvae were alone they were found in the warmest areas of the enclosures (Table 3; Fig. 2a). This was also true for larval bullfrogs when they were only with *R. aurora* larvae (Table 3; Fig. 2b). Overall, average water temperatures increased during the experiment (Table 3). The warmest water temperatures were found in the deep end of the enclosures for the first 2 weeks and then in the shallow ends for the remainder of the experiment (Table 3). When exposed to bullfrog larvae, *R. aurora* larvae used a different portion of the enclosures than when they were alone (Fig. 2a,b). Adult bullfrogs also influenced the habitat use of *R. aurora* larvae. After being introduced into the enclosures, adult bullfrogs remained active for 2 weeks (27 October to 10 November), and activity was not observed again until 20 March 1994 (week 7). When adult bullfrogs became active, the mean ranked distance from shore of both bullfrog and *R. aurora* larvae shifted from the shallow end of the enclosures to the deep end (Fig. 2c,d). *Rana aurora* larvae in the combined treatment had a mean ranked distance from the shore similar to that when they were with bull-

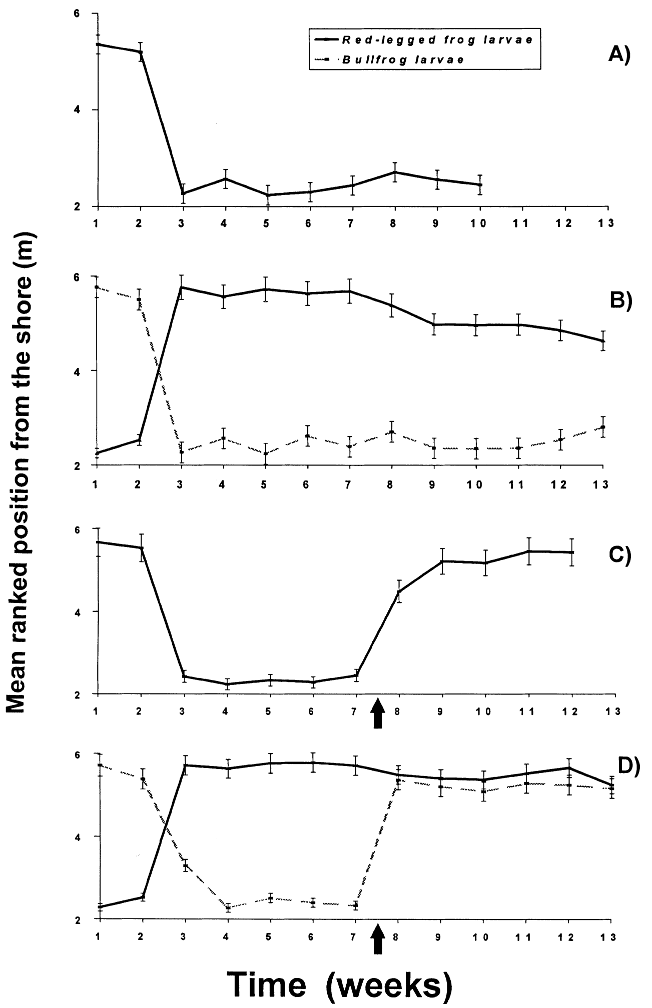

Figure 2. Mean ranked position (± 1 SE) of Rana aurora *tadpoles when alone (a), with* R. catesbeiana *larvae (b), with* R. catesbeiana *adults (c), and with both* R. catesbeiana *larvae and adults (d). Arrows indicate the start of adult activity.*

frog larvae only. Bullfrog larvae, however, also shifted position in response to adult activity. Thus, in the combined treatment the mircohabitat use of both species of larvae overlapped for the last 6 weeks of the experiment.

Experiment 2

Adult bullfrogs had significant effects on the survival of *R. aurora* metamorphs ($t_{11} = 4.7, p < 0.001$). Survival of metamorphs in the presence and absence of adult bullfrogs was 27.7% and 84.7%, respectively. All adult *R. catesbeiana* survived the experiment.

Experiment 3

Table 2. Results of repeated measures ANOVA on the effects of the presence of *Rana catesbeiana* larvae and adults on space use by red-legged frog tadpoles.

	df	F *ratio*	p
Between subjects			
adult	1	34.118	<0.0001
larvae	1	141.492	<0.0001
adult × larvae	1	87.102	<0.0001
error	8		
Within subjects			
time	9	21.785	<0.0001
time × adult	9	21.902	<0.0001
time × larvae	9	348.772	<0.0001
time × adult × larvae	9	25.169	<0.0001
error	72		

Both *R. catesbeiana* larvae and smallmouth bass influenced *R. aurora* growth, development, and survival (Table 4). We interpret these effects for each response variable employing the univariate tests and post hoc comparison (Tukey tests).

As in experiment 1, bullfrog larvae reduced mass at metamorphosis of *R. aurora* (Table 4; Fig. 3). Smallmouth bass, however, did not influence mass of *R. aurora*, either when alone or with bullfrog larvae (Tukey HSD $p = 0.47$). Mass was greatest for *R. aurora* when alone or with smallmouth bass alone than in any of the other treatments (Tukey HSD $p < 0.01$, Fig. 3).

Time to metamorphosis was similarly affected by bullfrog larvae and smallmouth bass. (Table 4; Fig. 3). Time to metamorphosis was fastest for *R. aurora* when alone or exposed to smallmouth bass only than in any of the other treatments (Tukey HSD $p < 0.01$; Fig. 3). There was no significant difference in time to metamorphosis for *R. aurora* between the bullfrogs only treatment and the combined treatment (Tukey HSD $p = 0.483$).

The combined effects of both larval bullfrogs and smallmouth bass influenced survival to metamorphosis of *R. aurora* (Table 4; Fig. 3). Survivorship was gener-

Table 3. Mean water temperature (°C) taken from 30 January 1994 to 1 May 1994 during the 24-hour trapping period for experiment 1.

	Distance from shore (m)		
Week	*2*	*4*	*6*
1	6.8	10.1	11.4
2	7.8	8.9	11.3
3	13.6	10.4	11.7
4	13.9	12.6	12.9
5	15.6	12.7	13.2
6	16.8	13.7	14.2
7	18.6	12.5	13.6
8	18.3	13.6	13.2
9	18.6	14.2	13.3
10	19.4	14.6	13.4
11	21.7	14.5	13.2
12	22.9	14.3	13.6
13	23.3	14.2	13.0

Table 4. Results of MANOVA for the overall effects of bullfrog larvae and smallmouth bass on *Rana aurora* tadpole growth, development, and survival, and ANOVAs for each response variable.

	F	*df*	p
MANOVA			
constant	9657.726	3, 6	<0.0001
bass	73.692	3, 6	<0.0001
bullfrog larvae	91.316	3, 6	<0.0001
bass × bullfrog	53.573	3, 6	0.003
ANOVAs*			
Mass			
bass	0.071	1, 8	0.796
bullfrog	89.623	1, 8	<0.0001
bass × bullfrog	0.210	1, 8	0.659
Time			
bass	1.47	1, 8	0.197
bullfrog	40.189	1, 8	<0.0001
bass × bullfrog	0.496	1, 8	0.501
Survival			
bass	272.283	1, 8	<0.0001
bullfrog	304.713	1, 8	<0.0001
bass × bullfrog	195.709	1, 8	<0.0001

**Response variables are proportion surviving (survival), mass at metamorphosis (mass), and time to metamorphosis (time). Significance level for univariate tests is 0.0125 (Bonferroni-adjusted for three response variables).*

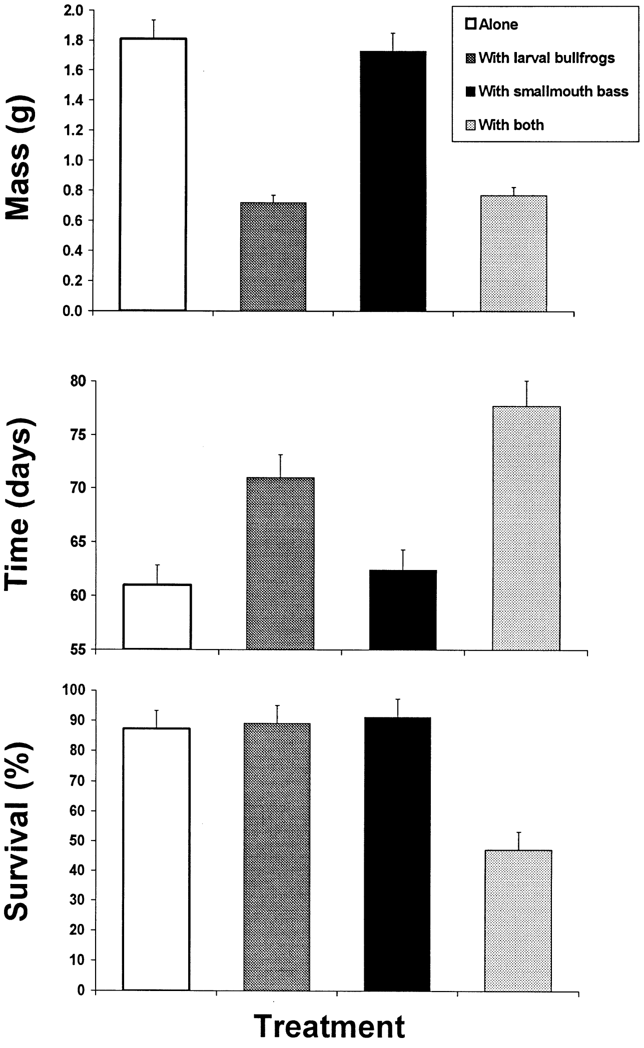

Figure 3. Mean (± 1 SE) mass at, time to, and survival to metamorphosis for Rana aurora *larvae exposed to larval* Rana catesbeiana *and smallmouth bass in field enclosures.*

ally high for *R. aurora* when alone or either with bullfrog tadpoles only or smallmouth bass only, averaging 87.3%, 89.1%, and 91.3%, respectively. The survivorship of *R. aurora*, however, decreased to 47.3% (Tukey HSD $p < 0.01$) in the presence of both larval bullfrogs and smallmouth bass. Survivorship for smallmouth bass and *R. catesbeiana* larvae was 100% and 97.4%, respectively.

Microhabitat use by larval *R. aurora* was significantly altered by the presence of larval bullfrogs and smallmouth bass (Table 5). Overall, microhabitat use by *R. aurora* larvae when alone or with bullfrog larvae was similar to that observed in experiment 1. When alone, *R. aurora* tended to be found in the warmest areas of the enclosure, which was also true for larval bullfrogs (Table 6; Fig. 4a,b). *Rana aurora* exposed only to smallmouth bass used a microhabitat similar to that used when they were alone. Their use of microhabitat, however, changed in the presence of both bullfrogs and bass compared to bullfrogs only (Table 5). The mean ranked distance from the shore of *R. aurora* in the combined treatment was not as high as in the bullfrog only treatment (Fig. 4b,d). This suggests that red-legged frog larvae responded to smallmouth bass, but only after they had moved into deeper water in the presence of bullfrogs.

Discussion

Our results show the negative effects on red-legged frogs of bullfrogs in conjunction with smallmouth bass. The presence of these species resulted in alteration of microhabitat use, slower growth, reduced development, and survivorship. Our experiments stress the importance of understanding the context-dependent nature of interactions between native and exotic species. In experiment 3, for example, smallmouth bass alone appeared to have little effect on *R. aurora*. Yet in the combined treatment bass had an effect on *R. aurora*. Similarly, in experiment 1, the combined treatments had the strongest effect on *R. aurora* larvae. Thus, the interaction between stages (larval-adult) or species (bullfrog-smallmouth bass) may produce indirect effects that are greater than when each factor is considered separately.

Amphibians have complex life cycles, which exposes them to a variety of possible interactions with invading species and, hence, a variety of ways to be adversely affected by invaders. This is especially true if the intro-

Table 5. Results of repeated measures ANOVA on the effects of the presence of *Rana catesbeiana* larvae and smallmouth bass on space use by red-logged frog tadpoles.

	df	F *ratio*	p
Between subjects			
bass	1	6.698	0.032
bullfrog	1	733.223	<0.0001
bass × bullfrog	1	7.713	0.024
error	8		
Within subjects			
source			
time	8	1.117	0.364
time × bass	8	1.246	0.287
time × bullfrog	8	1.220	0.302
time × bass × bullfrog	8	0.673	0.713
error	64		

duced species also has a complex life cycle. Thus, introduced species may produce a series of direct and indirect effects that can impact natives.

Microhabitat Use

The key feature in the interaction of bullfrogs with red-legged frogs appears to be the alteration of microhabitat use. Many studies have documented the behavioral responses of prey to the presence of their predators (Sih 1987; Petranka et al. 1987; Lima & Dill 1990; Wilson & Lefcort 1993; Kiesecker et al. 1996), indicating that such behavioral effects may be common. The mechanisms responsible for the shift in microhabitat use are likely based on behavioral responses. In fact, we have observed that *R. aurora* react to the presence of *R. catesbeiana* by retreating and reducing activity levels (Kiesecker & Blaustein 1997*b*).

Several hypotheses may account for the negative associations between bullfrog larvae and red-legged frog larvae. First, habitat partitioning may be a result of competition. Although tadpoles of different species may have similar feeding morphology and behavior (Duellmann & Trueb 1986), they may differ considerably in their rates of removal of food resources (Seale & Wassersug 1979). Tadpoles that forage more efficiently could cause those that forage less efficiently to leave an area. Several studies have shown that, through vigorous swimming and butting movements, larger larvae can monopolize clumped food resources and prevent smaller tadpoles from obtaining food (Savage 1952; Wilbur 1977). These behaviors may lead to tadpoles segregating by size into different microhabitats (Alford & Crump 1982; Alford 1986). Second, tadpoles may release substances that inhibit the growth and development of other larvae (Steinwascher 1978; Beebee & Wong 1992; Griffiths et al. 1993; Hayes et al. 1993). Thus, *R. aurora* tadpoles may avoid areas where chemical substances could hamper their growth. Third, larvae of *R. catesbeiana* consume tadpoles of other species (Ehrlich 1979). We have observed bullfrog larvae consuming hatchling *R. aurora*

Table 6. Mean water temperature (°C) taken from 1 February 1995 to 10 May 1995 during the weekly 24-hour trapping period for experiment 3.

	Distance from shore (m)		
Week	*2*	*4*	*6*
1	14.3	11.1	12.4
2	14.8	9.7	11.3
3	15.6	10.4	11.7
4	16.9	13.6	12.9
5	17.6	14.7	13.2
6	17.8	14.9	13.8
7	18.6	13.5	13.6
8	20.3	14.6	13.2
9	21.6	14.2	13.3
10	22.4	14.6	13.4

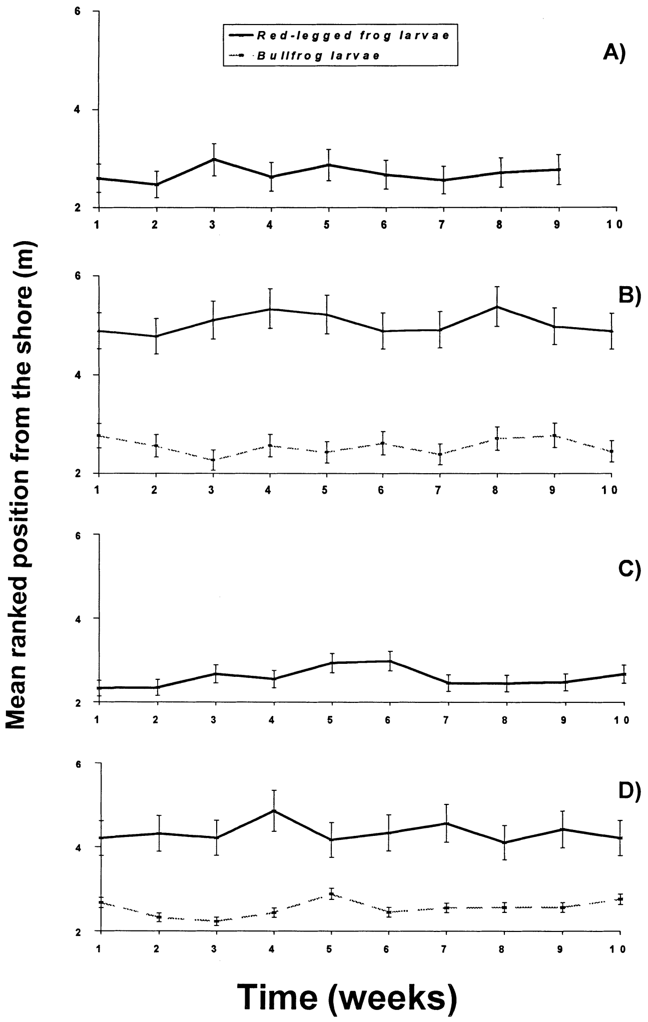

Figure 4. Mean ranked position (± 1 SE) of Rana aurora *tadpoles when alone (a), with* R. catesbeiana *larvae (b), with smallmouth bass (c), and with both* R. catesbeiana *larvae and smallmouth bass (d).*

under laboratory conditions (Kiesecker & Blaustein 1997*b*). If this occurs under natural conditions, it would provide an obvious reason for the observed avoidance behavior.

Increased activity of adult *R. catesbeiana* resulted in a shift of microhabitat use by both *R. aurora* and *R. catesbeiana* larvae. The activity of adult bullfrogs paralleled an increase in water temperature during the experiment. Larvae likely shifted position to avoid predation by adult *R. catesbeiana*. Adult *R. catesbeiana* are aquatic predators consuming a broad diversity of prey, including other amphibians (Corse & Metter 1980; Bury & Whelan 1986; Clarkson & DeVos 1986; Schwalbe & Rosen 1988; Beringer & Johnson 1995; Werner et al. 1995). The use of deep water by *R. aurora* in the presence of adult *R. catesbeiana* may be an effective way for tadpoles to avoid predation.

In contrast, *R. aurora* did not alter habitat use when exposed to smallmouth bass only, probably because smallmouth bass were only found in water deeper than 1 m. Thus, the emergent vegetation in the shallow end of the enclosures appeared to provide suitable refuge for *R. aurora* larvae. The response of *R. aurora* to bullfrogs, however, depended on the presence of bass. This suggests that *R. aurora* larvae respond to bass in situations where bass are capable of preying on them.

Growth and Development

Introduced aquatic predators and competitors may have strong effects on the development and growth rates of larval amphibians. Increased developmental time and decreased mass at metamorphosis can influence individual fitness and thus may ultimately affect populations. Aside from increasing the time that larvae are subjected to aquatic predators (Morin 1983), an extended larval period also can affect the post-metamorphic stage by leaving amphibians inadequate time to store fat for winter survival (Berven & Gill 1983). Smaller size at metamorphosis can decrease both survival and reproductive success in the terrestrial environment (Berven & Gill 1983; Woodward 1983, 1987; Smith 1987; Berven 1990; Scott 1994).

Larval *R. aurora* exhibited increased time to metamorphosis and decreased mass at metamorphosis when exposed to either larval or adult *R. catesbeiana*. These effects on *R. aurora* may be due to the shift in *R. aurora* habitat use induced by bullfrogs. In the presence of active adult bullfrogs, *R. aurora* larvae were found in the cooler deep water of the enclosures. Temperature may have strong effects on the growth and development of larval amphibians (Duellman & Trueb 1986), and cooler temperatures experienced by *R. aurora* may explain increases in developmental time. Reduced activity also is common for prey in the presence of predators (Sih 1987; Lima & Dill 1990; Sih & Kats 1994) and can result in reduced growth and increased developmental time (Skelly & Werner 1990; Skelly 1992). Also, microhabitats may differ in more ways than just temperature. For example, the quality and quantity of food present were also likely to be different. This difference in resources between microhabitats may influence *R. aurora* larvae because tadpoles are sensitive to the quality as well as the quantity of their diet (Kupferberg et al. 1994).

The influence of larval bullfrogs on *R. aurora* is difficult to interpret. Interspecific competition with bullfrog larvae can decrease the survivorship and growth of native tadpoles (Kupferberg 1997). In both experiments 1 and 3, *R. aurora* shifted habitat use in the presence of *R. catesbeiana* larvae. Thus, the reduced growth and increased time to metamorphosis experienced by *R. aurora* may be due to competition between the two species or a result of habitat alteration and the less favorable conditions associated with the alternate microhabitat.

Survival

Populations of native species may decline if introduced species affect their recruitment. Because of their complex life cycles, amphibians can potentially be influenced in both their aquatic and terrestrial environments. Survival of native amphibians could be affected in numerous ways by the concurrent introduction of bullfrogs and predatory fish. Attempts to assess any of these factors in isolation may overlook potential interactions that ultimately may explain native species losses.

In both experiments 1 and 3, survivorship of *R. aurora* was affected only in the combined treatments. In experiment 1 we do not know the specific causes of this mortality, but we presume that it was due to the synergistic effects of reduced activity in the presence of adult bullfrogs and low food resources due to overlap with larval bullfrogs. Both of these effects may lead to poorer conditions and increased chance of starvation. Although we cannot rule out predation by adult *R. catesbeiana,* we consider this unlikely because survival of red-legged frog larvae was not affected when they were exposed to adult bullfrogs only. The results of experiment 2, however, suggest that the influence of adult *R. catesbeiana* can be underestimated if the experiments are terminated at metamorphosis because survival of metamorphic *R. aurora* was greatly reduced in the presence of *R. catesbeiana* adults.

In experiment 3, the habitat shift of *R. aurora* in the presence of bullfrog larvae likely led to increased predation by smallmouth bass. Smallmouth bass were mainly observed in the deeper water of the enclosures. The shift in microhabitat use by *R. aurora* likely led to increased overlap between *R. aurora* and smallmouth bass. Bass (*Micropterus* sp.) are efficient predators of larval amphibians (Scott & Crossman 1973; Kruse & Francis 1977), and under laboratory conditions smallmouth bass readily consume *R. aurora* larvae (J. M. K., personal observation). Survivorship of larval *R. aurora* in experiments 1 and 3, however, was higher in all treatments than that experienced under natural conditions. This relatively high survivorship may be caused by enclosures excluding other natural predators (e.g., *Thamnophis* spp).

Predicting Invasion Impact

Biological invasions pose a threat to ecological communities and global biodiversity (Elton 1958; Mooney & Drake 1986; Drake et al. 1989; Lodge 1993). In particular, biological invasions pose a significant risk to freshwater biodiversity (Taylor et al. 1984; Master 1990; Allan & Flecker 1993). For example, introduced organisms have been associated with 68% of the 40 North American fish extinctions that have occurred in the 1900s (Miller et al. 1989). Bullfrogs may be of special interest because of their widespread introduction throughout the western United States and because they have been implicated in losses of native ranid frogs (Moyle 1973; Green 1978; Hammerson 1982; Clarkson & DeVos 1986). Bullfrogs have also been introduced into other regions of the world, including Italy (Albertini & Lanza 1987) and the Netherlands (Stumpel 1992), where they may have similar influences on other native species.

It is important to understand how introduced species affect native organisms so that we can predict invasion success (Lodge 1993). This may help in facing the challenge posed by the ever-growing rate at which organisms are introduced beyond their natural ranges and may also provide us with a better understanding of the factors involved in structuring communities.

Acknowledgments

We thank C. Miller, M. Anderson, and B. Edmond for providing technical assistance, and D. G. Hokit, S. Walls, S. Rothstein, G. McKenna, N. Santoro, and B. Sherbert for helpful discussions of experimental design. We thank the U.S. Forest Service Pacific Northwest Research Station, and especially D. Olson, for the use of vehicles. B. Menge, D. Olson, D. Chivers, E. Wildy, and A. Marco provided helpful suggestions on this manuscript. We thank the staff at the E. E. Wilson Wildlife Refuge for all the help they provided. Funding was provided by the Department of Zoology Research Funds and the National Science Foundation (Grant Number DEB-9423333).

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