POTENTIAL MECHANISMS UNDERLYING THE DISPLACEMENT OF NATIVE RED-LEGGED FROGS BY INTRODUCED BULLFROGS

JOSEPH M. KIESECKER,[1,4] ANDREW R. BLAUSTEIN,[2] AND CHERI L. MILLER[3]

[1]*Department of Biology, Pennsylvania State University, 208 Mueller Lab, University Park, Pennsylvania 16802-5301 USA*
[2]*Department of Zoology, Oregon State University, Corvallis, Oregon 97331 USA*
[3]*Alexion Pharmaceuticals Inc., 25 Science Park, Suite 360, New Haven, Connecticut 06511 USA*

Abstract. The bullfrog (*Rana catesbeiana*) is a widespread invasive species that may displace several species of native ranid frogs throughout its introduced range. Although this pattern is well known, the underlying mechanism of displacement remains unclear. Previous work has suggested that interactions with bullfrogs may contribute to the population decline of native red-legged frogs (*Rana aurora*) in Oregon, USA. Interactions between these species appear to be strongly context dependent and potentially influenced by habitat modification. To gain a more detailed understanding of this displacement, we studied the effects of food-resource distribution, a factor that can be influenced by human habitat alteration, on competitive interactions between larval red-legged frogs and larval bullfrogs.

The presence of bullfrog larvae had strong negative effects on the performance of red-legged frog larvae. However, this effect was dependent on whether food resources were clumped or scattered. Survivorship to metamorphosis and mass at metamorphosis were reduced when red-legged frog tadpoles were exposed to bullfrogs in clumped-resource ponds. In contrast, the presence of bullfrogs had a negligible effect on larval performance of red-legged frogs in scattered-resource ponds.

Behavioral observations indicate that a passive interference mechanism is likely to be responsible for the outcome of interactions between bullfrogs and red-legged frogs. Our results suggest that clumped resources can intensify interspecific competition, and this may influence the success of exotics when human-induced habitat alteration affects resource distribution. Understanding the context-dependent nature of interactions will be necessary if we are to predict invasion success and control the impact of exotics on natives.

Key words: anuran larvae; competition; exotics; higher-order interactions; interspecific competition; introduced species; Rana aurora; Rana catesbeiana.

INTRODUCTION

The study of invading species has been of considerable interest to ecologists since Elton's (1958) classic book, *The Ecology of Invasions.* For the past several decades, the search for generality in invasion biology research has focused on attempts to identify attributes of highly invasive species (e.g., Bazzaz 1986, Newsome and Noble 1986), or the characteristics of communities that make them susceptible to invasion (e.g., Orians 1986, Crawley 1987). Despite considerable effort, predicting the outcome of particular invasions has proved difficult at best (Moulton and Pimm 1986, Crawley 1987). Following a more reductionist approach to community ecology (Schoener 1986), a renewed interest has been placed on studying the context in which invasions are possible, and identifying the mechanisms controlling invasion success, using an experimental approach (Lodge 1993).

Until recently, experimental studies examining the mechanisms of invasions have been rare (e.g., Petren et al. 1993; see discussion in Kareiva 1996). However,

recent studies have conducted manipulative experiments to examine the factors controlling invasions (Bergelson et al. 1993, D'Antonio 1993), and the mechanisms underlying the displacement of native species (Petren et al. 1993, Petren and Case 1996, 1998, Thebaud et al. 1996, Kiesecker and Blaustein 1997, 1998, Kupferburg 1997, Holway et al. 1998, Juliano 1998, Holway 1999). Although rare, these experimental approaches are essential to understanding the basis of invasion success (Kareiva 1996).

One of the few generalizations to emerge from detailed studies of invasion biology is the relationship between disturbance and invasion success (Drake et al. 1989). This work suggests that environments subjected to disturbance are also prone to invasion. This concept follows from the observation that introduced species are common in highly disturbed areas (e.g., roadsides; Amor and Stevens 1976), and are able to displace natives in human-made habitats, but unable to replace natives in relatively undisturbed habitats (e.g., Herbold and Moyle 1986). Despite the entrenchment of this concept, few studies have examined how disturbance alters interactions between natives and introduced species (but see Bergelson et al. 1993, Burke and Grime 1996, Suarez et al. 1998). In this study we use an experi-

mental approach to examine how resource distribution, associated with human-induced habitat disturbance, can influence competitive interactions between larvae of the native red-legged frog, *Rana aurora,* and the introduced bullfrog, *Rana catesbeiana.*

Numerous workers (e.g., Moyle 1973, Bury and Luckenbach 1976, Fisher and Shaffer 1996, Hayes and Jennings 1996, Kupferburg 1997) have reported population declines of ranid frogs native to the western United States. However, the impact of bullfrogs on native frogs is often unclear because of concurrent introductions of predatory fish and habitat modifications (Kiesecker and Blaustein 1998, Adams 1999). Habitat modifications that reduce or alter the distribution of essential microhabitat can potentially alter the outcome of interactions between red-legged frogs and bullfrogs. Red-legged frog larvae react to the presence of larval and adult bullfrogs by retreating and reducing activity levels (Kiesecker and Blaustein 1997). Under field conditions, these behavioral changes result in microhabitat shifts by red-legged frog larvae (Kiesecker and Blaustein 1998).

In western North America, dredging, damming, and mitigation frequently replace large, shallow, ephemeral wetlands with smaller permanent ponds (Hayes and Jennings 1986, Kentula et al. 1992, Holland et al. 1995, Richter et al. 1997). These smaller permanent ponds tend to contain less shallow water and emergent vegetation (Hayes and Jennings 1986, Richter and Azous 1995, Adams 1999); in addition, the presence of emergent vegetation tends to be clumped along a narrow area at the edge of the pond. We predicted that clumping resources would intensify interspecific competition between red-legged frogs and bullfrogs. To test this hypothesis we conducted an artificial pond experiment where we manipulated the density of red-legged frog and bullfrog larvae, and the distribution of food resources.

We made three predictions regarding interspecific competition between red-legged frogs and bullfrogs. First, we predicted that the presence of bullfrog larvae would have negative effects on the growth and development of red-legged frog larvae, and that this effect would be much stronger when food resources were clumped. Our prediction was based on asymmetries in age, development stage, and size between individuals of these two species (i.e., bullfrogs are older and larger by the time the two species begin to interact), and the influence this is likely to have on competitive interactions (e.g., Wilbur 1987, Alford 1989, Kiesecker and Blaustein 1997). In addition, clumped resource distributions may intensify interspecific competition in a number of systems (Maurer 1984, Brown and Munger 1985, Sexton 1990). Second, we predicted that red-legged frog larvae would spend less time active and feeding in the presence of bullfrog larvae. We based this prediction on observations that red-legged frog larvae reduced activity and avoided areas that contain bullfrog larvae (Kiesecker and Blaustein 1997). Finally, we predicted that bullfrog larvae would employ behavioral interference competition, and that this interference may be more severe in situations with clumped resources. We based this final prediction on the assumption that moving toward another individual is a form of interference competition (Walls 1990, Faragher and Jaeger 1998).

MATERIALS AND METHODS

We manipulated the presence of bullfrog larvae and red-legged frog larvae in replicated artificial ponds. These ponds were located in a field at the Oregon State University Agricultural Station (6.4 km east of Corvallis, Benton County, Oregon, USA). Experiments were conducted during the natural breeding season of red-legged frogs, from 6 February to 21 April 1995. We created pond communities in plastic pools 1.5 m in diameter, filled with water to a depth of ~20 cm. Ponds contained approximately 150 L of water, and were covered with fiberglass screen lids to prevent colonization by frogs, invertebrates, and other organisms. The screen lids also retained metamorphosed amphibians until their collection and processing, to examine mass at, time to, and survival to metamorphosis.

We used a fully factorial design that crossed the presence of red-legged frog larvae (alone or with bullfrog larvae) at two natural densities: low (16 larvae/pool; 0.106 larvae/L), and high (32 larvae/pool; 0.213 larvae/L). These densities are comparable to natural densities of both species, which varies from 0.05 to 1.8 larvae/L (J. M. Kiesecker, *unpublished data*). We also crossed these treatments with food resources that were either clumped or scattered, and the resulting eight treatments were replicated five times for a total of 40 pools. Treatments were randomly assigned to tanks within five spatial blocks.

To provide food for developing larvae, we added 15 g of pelleted Purina Rabbit Chow (Purina Mills, Gray Summit, Missouri, USA) to each pool. To limit algae growth, which may confound the resource-distribution treatment, pools were drained, cleaned, and restocked with food every third week. During cleaning, tadpoles were captured with a net and held in 40 L of dechlorinated tap water. After cleaning, tadpoles were placed back into their original pools. The clumped-resource treatment was created by placing all 15 g of pelleted rabbit chow into a center feeding station. Feeding stations consisted of a 15 cm diameter plastic plate, which provided free access to food resources, but limited their distribution to one central location. The scattered-resource regime placed an equivalent amount of pelleted rabbit chow homogeneously within the ponds.

Red-legged frogs used in the experiment were collected as six newly oviposited clutches (Gosner Stage 1–4; Gosner 1960). Embryos were transported to our laboratory, where they were placed into aerated 38-L aquaria filled with dechlorinated tap water. Hatchling

JOSEPH M. KIESECKER ET AL.

(Gosner stage 23; Gosner 1960) red-legged frogs were kept in the lab for 2 wk prior to use in experiments, to obtain a size that would prevent predation by bullfrog larvae (Kiesecker and Blaustein 1997). To minimize potential genetic effects, we added hatchlings from each of six different clutches to each pond. Bullfrogs used in this study were collected as first-year larvae (Gosner stage 25; Gosner 1960). Upon collection, tadpoles were transported to the lab and maintained on a diet of rabbit chow.

Tadpoles of each species were added to the ponds on 6 February 1995. Ponds were followed through larval development of red-legged frogs, and we removed individuals from the pools as they metamorphosed (front limb emergence; Gosner stage 42; Gosner 1960), and recorded mass (to the nearest milligram) at, and time (in days) to, metamorphosis. We terminated the experiment when all red-legged frog tadpoles had either metamorphosed or died. No bullfrogs reached metamorphosis during the experiment.

Behavioral observations

To quantify the potential mechanisms underlying competitive interactions between bullfrog and red-legged frog larvae, we assayed behavior of red-legged frogs used in the experiment. On three occasions (22 February, 21 March, 15 April 1995) red-legged frog tadpoles in each pool were observed for 4-min periods. In the first 2 min we recorded the activity of tadpoles within each pond. We measured activity by recording the total time, in seconds, that any of the red-legged frog tadpoles were moving. During the second 2-min period, we recorded the total time that any of the red-legged frogs were feeding (scraping at a surface with the mouthparts). Ponds with clumped food resources were observed for an additional 2-min period, where we recorded the number of red-legged frog tadpoles that entered the central feeding station. In addition, ponds with bullfrogs were observed for an additional 2 min, and we noted aggressive (bumping, moves towards; Faragher and Jaeger 1998) behavior that bullfrogs directed at red-legged frog tadpoles.

We conducted a total of 360 2-min observations. The order in which ponds were observed was randomly determined. We conducted observations during daylight hours between 1100 and 1630. Because observations of the same pond may be considered pseudoreplicates, we calculated the average activity, feeding, and number in the central feeding station, and aggressive behavior, for the three observation periods of each pond.

Statistical analyses

We used multivariate analysis of variance (MANOVA) to test for the effects of independent factors, including density (high or low), bullfrogs (present or absent), and food resources (clumped or scattered), on the dependent variables of mean time to, mean mass

at, and mean survivorship to metamorphosis of red-legged frogs (Tabachnick and Fidell 1989). After MANOVA, we used a Bonferroni-adjusted univariate analysis of variance (ANOVA) on each response variable to help assess which variables were responsible for significant main effects. ANOVA was also used to test for the effect of bullfrogs (present or absent), density (low or high), and resource distribution on the amount of time spent feeding by red-legged frog tadpoles. An additional analysis, comparing the time spent moving, used a comparable ANOVA structure. We used a Student's t test to compare the effects of bullfrogs on the mean number of red-legged frog tadpoles within the central feeding stations in the clumped food resource treatments. We also used a Student's t test to compare the effects of food distribution on the number of times bullfrog tadpoles swam toward a red-legged frog tadpole. A preliminary analysis indicated no significant block effect. Therefore, the block and error terms were pooled for remaining tests. Because individuals in ponds were not independent of one another, all variables were analyzed as pond means. We arcsine transformed the data on survivorship before the analysis; after transformation, the data met the parametric assumptions. For all other dependent variables, parametric assumptions were met without transformations.

RESULTS

The results of our MANOVA revealed strong main effects of bullfrogs and resource distribution on red-legged frog performance (Table 1). There was also a nonsignificant trend indicating that density had a small influence on tadpole performance (Table 1). In addition, there was a strong interaction between bullfrog presence and resource distribution (Table 1). In the following section we use univariate tests (ANOVA) and post hoc comparisons (Tukey tests) to interpret patterns of response of size, developmental time, and survival due to our manipulations.

Red-legged frogs in clumped-resource ponds were significantly affected by bullfrog presence for each of the response variables measured (Table 1, Fig. 1). Red-legged frogs emerging from ponds with clumped resources were 25.9% smaller than their counterparts in ponds containing no bullfrogs (Tukey hsd, $P < 0.031$). Similarly, tadpoles in clumped resource ponds containing bullfrogs took 6.9 d longer to reach metamorphosis compared to individuals in ponds without bullfrogs (Tukey hsd, $P < 0.01$). Finally, the number of animals reaching metamorphosis in clumped-resource ponds was also lower for red-legged frogs exposed to bullfrogs, compared to those in ponds without bullfrogs (Tukey hsd, $P < 0.041$). Among animals in the clumped resource treatments, only 55.5% of red-legged frogs exposed to bullfrogs completed metamorphosis, compared to 71.2% survivorship among tadpoles not exposed to bullfrogs.

In marked contrast to patterns seen in clumped-re-

TABLE 1. Results of MANOVA for overall effects of bull-frogs, food distribution, and density, on red-legged frog larvae survival to metamorphosis, mass, and time to meta-morphosis, and ANOVAs for each response variable.

Variables	F	df	P
MANOVA			
Constant	2437.42	3, 30	<0.0001
Bullfrogs	6.700	3, 30	0.001
Food	8.077	3, 30	<0.0001
Density	2.321	3, 30	0.095
Bullfrogs × food	4.552	3, 30	0.01
Bullfrogs × density	0.827	3, 30	0.489
Food × density	0.779	3, 30	0.515
Bullfrogs × food × density	1.114	3, 30	0.359
ANOVAs			
Mass			
Bullfrogs	9.185	1, 32	0.005
Food	9.027	1, 32	0.005
Time			
Bullfrogs	7.931	1, 32	0.008
Food	8.686	1, 32	0.006
Survival			
Food	8.430	1, 32	0.007
Bullfrogs × food	8.430	1, 32	0.007

Notes: Response variables are mass at metamorphosis (mass), time to metamorphosis (time), and proportion sur-viving to metamorphosis (survival). For simplicity we have only included ANOVA comparisons that are significant. The significance level for univariate tests is 0.0125 (Bonferroni-adjusted for three response variables).

source ponds, we found very little impact of bullfrogs on red-legged frogs in scattered-resource ponds. Nei-ther mass at, time to, nor survival to metamorphosis was affected by bullfrog presence (Table 1, Fig. 1).

Behavioral observations

The results of our ANOVA indicated strong effects of bullfrogs on both red-legged frog activity and feed-ing (Table 2, Fig. 2). Time spent feeding was also in-fluenced by an interaction between bullfrog presence and resource distribution. Red-legged frog tadpoles were less likely to be active and feeding in the presence of bullfrog tadpoles. Bullfrog-induced reduction in feeding by red-legged frog tadpoles was more pro-nounced in clumped-resource ponds (Fig. 2). In addi-tion, red-legged frog tadpoles in clumped-resource ponds were less likely to be found within the central feeding station in ponds containing bullfrog tadpoles, compared to ponds without bullfrogs ($t_{18} = 5.404$; $P < 0.001$; mean number of red-legged frog tadpoles in the central feeding station ± 1 SE: with bullfrogs, 3.40 ± 1.284 red-legged tadpoles; without bullfrogs, 18.8 ± 2.542 red-legged tadpoles). We observed several cas-es of bumping and harassing by bullfrog tadpoles. Ob-servations of harassment were more likely to occur in and around food. However, there were no differences in the number of moves toward a red-legged frog tad-pole made by bullfrog tadpoles in ponds with clumped resources compared with scattered resource ponds

($t_{18} = 0.075$, $P = 0.941$; mean number of moves toward clumped resources [± 1 SE] = 4.09 ± 1.89; mean num-ber of moves toward scattered resources = 4.150 ± 1.66).

DISCUSSION

In reviews of community characteristics associated with invasion, disturbance is consistently associated with the presence of alien species (Elton 1958, Crawley 1987, Drake et al. 1989). However, the precise effects of disturbance are rarely documented (Hobbs 1989, D'Antonio 1993). Disturbance may remove natural en-emies that prevent invasion, eliminate competitively superior native species, and/or may alter the resource base in ways that favor the exotic species. Our results suggest the latter may be true for interactions between larval bullfrogs and red-legged frogs.

We found that manipulating the distribution of food resources can alter the outcome of competition between red-legged frogs and bullfrogs. Relative to controls, we found that red-legged frog tadpoles exposed to bull-frogs in clumped-resource environments grew 25.9% slower, and that 22.1% fewer survived to metamor-phosis. In contrast, we found that the impacts of bull-
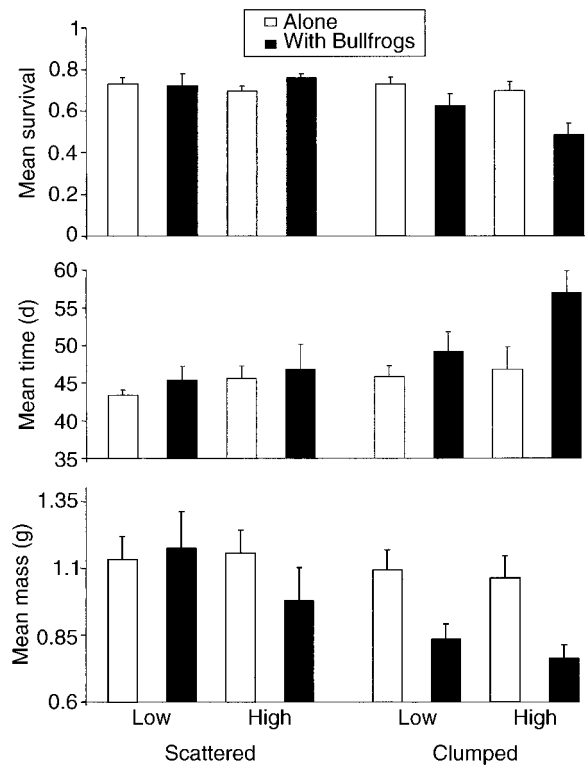

FIG. 1. Summary of the effects of food-resource distri-bution (clumped or scattered) and bullfrogs on the mean sur-vival (survival to metamorphosis), mean time (time to meta-morphosis), and mean mass (mass at metamorphosis) of red-legged frogs, *Rana aurora*. Bars represent the mean + 1 SE ($N = 5$). Initial densities of red-legged frogs are indicated as Low or High.

TABLE 2. Results of ANOVA for effects of bullfrogs, food distribution, and density, on larval red-legged frog time active (Activity) and time spent feeding (Feeding).

Variables	F	df	P
Activity			
Bullfrogs	44.415	1, 32	<0.0001
Food	0.653	1, 32	0.425
Density	0.235	1, 32	0.631
Bullfrogs × food	1.169	1, 32	0.212
Bullfrogs × density	0.069	1, 32	0.795
Food × density	0.180	1, 32	0.674
Bullfrogs × food × density	0.471	1, 32	0.497
Error	245.188		
Feeding			
Bullfrogs	81.893	1, 32	<0.0001
Food	8.788	1, 32	0.006
Density	0.298	1, 32	0.589
Bullfrogs × food	10.993	1, 32	0.002
Bullfrogs × density	0.184	1, 32	0.671
Food × density	0.083	1, 32	0.847
Bullfrogs × food × density	0.609	1, 32	0.441
Error	65.725		

frogs on red-legged frogs were negligible when tadpoles were raised in a scattered-resource environment. Concordant with our initial hypothesis, we found that clumped-resource environments enhanced the strength of competition between bullfrogs and red-legged frog larvae. In a number of other studies, clumped food resource distributions seem to intensify interspecific competition (e.g., chipmunks, Brown 1971; birds, Maurer 1984; wasps, Moller et al. 1989; geckos, Petren and Case 1996), suggesting that this may be a common phenomenon.

Our design provided insights regarding the specific mechanism by which amphibian performance was affected during the experiment. Red-legged frogs in both scattered and clumped-resource ponds reduced the amount of time they were active and the amount of time they spent feeding, when in the presence of bullfrogs. In clumped-resource pools, red-legged frogs reduced the amount of time they were in the central feeding pit when bullfrogs were present. However, in scattered-resource pools, where food was evenly distributed, red-legged frogs were able to spend a greater percentage of active time involved in feeding. We suggest that a passive interference mechanism (Maurer 1984), whereby subordinate red-legged frog larvae avoid bullfrogs, is responsible for the observed outcome. Direct interference during foraging may have some effect, but there were no differences in the number of aggressive encounters between bullfrogs and red-legged frogs in clumped and scattered ponds. The decrease in performance of red-legged frogs in clumped-resource ponds is likely the result of their inability to feed while avoiding areas that contain bullfrogs. In contrast, red-legged frogs in scattered-resource ponds were able to avoid bullfrogs and still maintain a relatively high level of feeding. Alternatively, decreased performance experienced by red-leg-

ged frogs in the presence of bullfrogs could be the results of shared pathogens. Bullfrogs may harbor pathogens that could influence performance of native ranid frogs. Nevertheless, without more detailed analysis we feel it is premature to provide any definitive estimate regarding the importance of pathogens in bullfrog and red-legged frog interactions. However, the behavioral responses of red-legged frogs to bullfrogs could be indicative of a behavioral reduction of infection risk (see Kiesecker et al. 1999).

Our data may provide insight into the mechanism that may be important in the displacement of native red-legged frogs by introduced bullfrogs. Because bullfrogs breed in midsummer and larvae overwinter, tadpoles of red-legged frogs are both smaller and less developed by the time the two species begin to interact. Bullfrog tadpoles, therefore, may use this size and developmental stage asymmetry to their advantage by consuming newly hatched larvae of red-legged frogs (Kiesecker and Blaustein 1997). Red-legged frogs that survive predation may then be harassed by bullfrogs. The harassment may increase the amount of time that red-legged frogs avoid bullfrogs, and decrease the amount of time that red-legged frogs spend feeding (Kiesecker and Blaustein 1997, 1998). This alteration of red-legged frog behavior can eventually lead to a decrease in both growth and survival of red-legged frog tadpoles (Kiesecker and Blaustein 1998). In addition
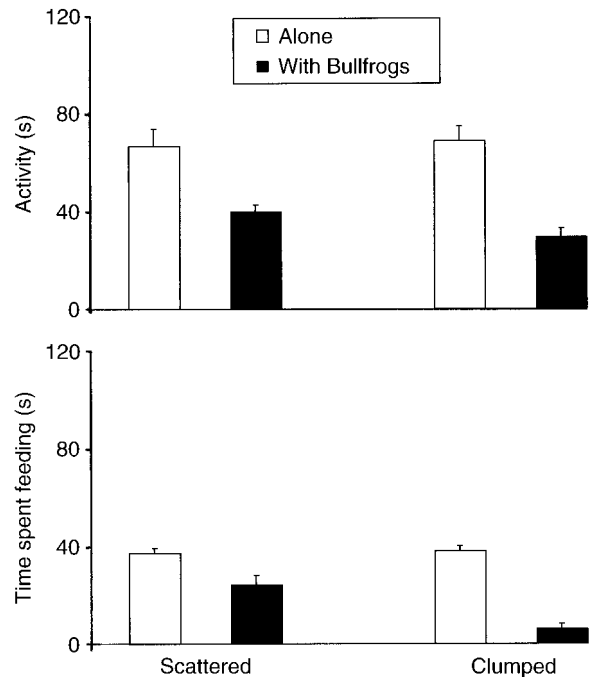

FIG. 2. Summary of the effects of bullfrogs (absent or present) and food resource distribution (clumped or scattered) on the mean activity (total time any red-legged frog was moving) and mean time spent feeding (total time that any red-legged frog was feeding) of red-legged frogs, *Rana aurora.* Bars represent the mean + 1 SE ($N = 5$).

to intensifying competition between tadpoles, clumping and/or reducing microhabitat may alter native species capacity to avoid predation (Kiesecker and Blaustein 1998). In fact, the presence of bullfrogs is often coupled with that of introduced predatory fish, and impacts that bullfrogs have on native frogs are likely a complicated blend of both competition and predation (Kiesecker and Blaustein 1998, Adams 1999).

In western North America, modification of wetlands frequently reduces the suitability of habitat for native frog species while benefiting introduced bullfrogs (Hayes and Jennings 1986, Richter and Azous 1995, Adams 1999). For example, large, shallow, ephemeral wetlands are commonly converted to smaller permanent ponds (Kentula et al. 1992, Holland et al. 1995, Richter et al. 1997, Adams 1999). These changes provide the conditions needed for successful breeding by bullfrogs. Permanent conditions can also increase the number and types of predators that may be present (Wellborn et al. 1996). These smaller permanent ponds tend to contain less shallow water and emergent vegetation, and the presence of emergent vegetation tends to be clumped along a narrow area at the edge of the pond.

Surveys of 42 historical breeding sites in the Willamette Valley of Oregon (J. M. Kiesecker, *unpublished data*) indicate that red-legged frogs are absent from 69% of their original historical sites. Occupied sites tend to differ from unoccupied sites in a number of ways. Occupied sites tend to have a higher percentage (mean = 40.6%) of shallow water (<20 cm) with emergent vegetation, compared with unoccupied sites (mean = 15.1%). In addition, 24 out of 29 of the unoccupied sites contained a breeding population of bullfrogs compared to only seven out of 13 of the occupied sites. However, neither bullfrog presence nor amount of emergent vegetation alone appears to explain occupancy patterns. For example, in the absence of bullfrogs, red-legged frogs occupy sites with as little as 5.7% emergent vegetation. In addition, coexistence of these two species has been observed at 16.6% of the sites. However, sites where the two species currently coexist also have a high percentage (mean = 48%) of emergent vegetation and shallow water. Areas with shallow water and emergent vegetation may be an essential microhabitat, because these areas will likely have warmer temperatures and high algal productivity, which will benefit growth of amphibian larvae (Kiesecker and Blaustein 1998). The results of our study indicate that resource distribution can have strong effects on interactions between larval red-legged frog and bullfrogs. Thus, habitat modification that results in clumped resources may favor bullfrog persistence and displacement of red-legged frogs.

The results of this study are also of general interest to the understanding of biological invasions. Controlling invasive species has mainly focused on eradicating exotics or attempting to control their population sizes through the use of biological control agents. Both of these methods have had limited success, and in some cases have resulted in the introduction of additional pest species (Simberloff and Stiling 1996). Understanding the context-dependent nature of invasion may allow the development of strategies to prevent successful invasion and develop systems that limit the impact of exotics on native species.

The results of interactions among red-legged frogs and bullfrogs (Kiesecker and Blaustein 1997, 1998) parallel recent work on interactions between native and exotic species in other systems (e.g., house geckos on Pacific islands; Petren et al. 1993, Petren and Case 1996). In both cases, human environmental changes that redistributed resources also altered competitive interactions in favor of the exotic species. Human-induced habitat modification may be perceived by some species as resource clumps; these species may be able to exploit these clumps to the disadvantage of other, possibly native, species. More work will be needed to assess the general importance of how human development alters the distribution of resources, and how this can alter interactions between native and exotic species. We stress the importance of understanding the context-dependent nature of interactions between introduced and native species, if we are to predict invasion success and control the impact of exotics on natives.

LITERATURE CITED

Adams, M. J. 1999. Correlated factors in amphibian decline: exotic species and habitat change in Western Washington. Journal of Wildlife Management **63**:1162–1171.

Alford, R. A. 1989. Effects of parentage and competitor phenology on the growth of larval *Hyla chrysoscelis*. Oikos **54**:325–330.

Amor, R. L., and P. L. Stevens. 1976. Spread of weeds from a roadside into sclerophyll forest at Dartmouth, Australia. Weed Research **16**:111–118.

Bazzaz, F. A. 1986. Life history of colonizing plants: some demographic, genetic and physiological features. Pages 96–110 *in* H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.

Bergelson, J., J. A. Newman, and E. M. Floresroux. 1993. Rates of weed spread in spatially heterogeneous environments. Ecology **74**:999–1011.

Brown, J. H. 1971. Mechanisms of competitive exclusion between two species of chipmunk. Ecology **52**:305–311.

Brown, J. H., and J. C. Munger. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. Ecology **66**:1545–1563.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology **77**:776–790.

Bury, R. B., and R. A. Lunkenbach. 1976. Introduced amphibians and reptiles in California. Biological Conservation **10**:1–14.

Crawley, M. J. 1987. What makes a community invasible? Pages 429–453 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, succession and stability. Blackwell Scientific, London, UK.

D'Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. Ecology **74**:83–95.

Drake, J., F. DiCastri, R. Groves, F. Kruger, H. Mooney, M. Rejmanek, and M. Williamson, editors. 1989. Biological invasions: a global perspective. Wiley and Sons, Chichester, UK.

Elton, C. E. 1958. The ecology of invasions by animals and plants. Chapman and Hall, New York, New York, USA.

Faragher, S. G., and R. G. Jaeger. 1998. Tadpole bullies: examining mechanisms of competition in a community of larval anurans. Canadian Journal of Zoology **76**:144–153.

Fisher, R. N., and H. B. Shaffer. 1996. The decline of amphibians in California's great Central Valley. Conservation Biology **10**:1387–1397.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica **16**:183–190.

Hayes, M. P., and M. R. Jennings. 1986. Decline of ranid frog species in Western North America: are bullfrogs (*Rana catesbeiana*) responsible? Journal of Herpetology **20**:490–509.

Herbold, B., and P. B. Moyle. 1986. Introduced species and vacant niches. American Naturalist **128**:751–760.

Hobbs, R. J. 1989. The nature and effects of disturbance relative to invasions. Pages 389–405 *in* J. A. Drake, F. DiCastri, R. H. Groves, and F. J. Kruger, editors. Biological invasion: a global perspective. Wiley and Sons, New York, New York, USA.

Holland, C. C., J. Honea, S. E. Gwin, and M. E. Kentula. 1995. Wetland degradation and loss in the rapidly urbanizing area of Portland, Oregon. Wetlands **15**:336–345.

Holway, D. A. 1999. Competitive mechanisms underlying the displacement of native ants by invasive argentine ant. Ecology **80**:238–251.

Holway, D. A., A. V. Suarez, and T. J. Case. 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. Science **282**:949–952.

Juliano, S. A. 1998. Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition? Ecology **79**:255–268.

Kareiva, P., editor. 1996. Developing a predictive ecology for non-indigenous species and ecological invasions. Ecology **77**:1651–1697.

Kentula, M. E., J. C. Sifneos, J. W. Good, M. Rylko, and K. Kunz. 1992. Trends and patterns in section 404 permitting requiring compensatory mitigation in Oregon and Washington, USA. Environmental Management **16**:109–119.

Kiesecker, J. M., and A. R. Blaustein. 1997. Population differences in responses of *Rana aurora* to introduced *Rana catesbeiana*. Ecology **78**:1752–1760.

Kiesecker, J. M., and A. R. Blaustein. 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., D. K. Skelly, K. H. Beard, and E. Preisser. 1999. Behavioral reduction of infection risk. Proceedings of the National Academy of Sciences (USA) **96**:9165–9168.

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

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**:133–137.

Maurer, B. A. 1984. Interference and exploitation in bird communities. Wilson Bulletin **96**:380–395.

Moller, H., A. V. Tilley, B. W. Thomas, and P. D. Gase. 1989. Effects of introduced social wasps on the standing crop of honeydew in New Zealand beech forests. New Zealand Journal of Zoology **18**:171–179.

Moulton, M. P., and S. L. Pimm. 1986. Species introductions to Hawaii. Pages 231–249 *in* H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.

Moyle, P. B. 1973. Effects of introduced bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. Copeia 1973(1–4):18–22.

Newsome, A. E., and I. R. Noble. 1986. Ecological and physiological characteristics of invading species. Pages 1–20 *in* R. H. Groves and J. J. Burdon, editors. Ecology of biological invasions: an Australian perspective. Australian Academy of Sciences, Canberra, Australia.

Orians, G. H. 1986. Site characteristics favoring invasion. Pages 133–148 *in* H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.

Petren, K., D. Bolger, and T. J. Case. 1993. Mechanisms in the competitive success of an invading sexual gecko over an asexual native. Science **259**:354–358.

Petren, K., and T. J. Case. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. Ecology **77**:118–132.

Petren, K., and T. J. Case. 1998. Habitat structure determines competition intensity and invasion success in gecko lizards. Proceedings of the National Academy of Sciences (USA) **95**:11739–11744.

Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology **11**:1081–1093.

Richter, K. O., and A. L. Azous. 1995. Amphibian occurrence and wetland characteristics in the Puget Sound basin. Wetlands **15**:305–312.

Schoener, T. W. 1986. Mechanistic approaches to community ecology: a new reductionism. American Zoologist **26**:81–106.

Sexton, O. J. 1990. Replacement of fox squirrels by gray squirrels in a suburban habitat. American Midland Naturalist **124**:198–205.

Simberloff, D., and P. Stiling. 1996. How risky is biological control? Ecology **77**:1965–1974.

Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal Southern California. Ecology **79**:2041–2056.

Tabachnick, B. G., and L. S. Fidell. 1989. Using multivariate statistics. Harper Collins, New York, New York, USA.

Thebaud, C., A. C. Finzi, L. Affre, M. Debussche, and J. Escarre. 1996. Assessing why two introduced *Conyza* differ in their ability to invade Mediterranean old fields. Ecology **77**:791–804.

Walls, S. C. 1990. Interference competition in postmetamorphic salamanders: interspecific differences in aggression by coexisting species. Ecology **71**:307–314.

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics **27**:337–363.

Wilbur, H. M. 1987. Regulation of structure in complex systems: experimental temporary pond communities. Ecology **68**:1437–1452.