CORRELATED FACTORS IN AMPHIBIAN DECLINE: EXOTIC SPECIES AND HABITAT CHANGE IN WESTERN WASHINGTON

MICHAEL J. ADAMS,[1,2] University of Washington, College of Forest Resources, Seattle, WA 98195, USA

Abstract: Amphibian declines may frequently be associated with multiple, correlated factors. In western North America, exotic species and hydrological changes are often correlated and are considered 2 of the greatest threats to freshwater systems. Bullfrog (*Rana catesbeiana*) introductions are frequently cited as a threat to lentic-breeding anurans native to western North America and are a suspected factor in the decline of red-legged frogs (*Rana aurora*) in California. Introduced fish and habitat change are cited less frequently but are equally viable hypotheses. I examined the relation among introduced species, habitat, and the distribution and abundance of red-legged frogs in western Washington. Red-legged frog occurrence in the Puget Lowlands was more closely associated with habitat structure and the presence of exotic fish than with the presence of bullfrogs. The spread of exotics is correlated with a shift toward greater permanence in wetland habitats regionally. Conservation of more ephemeral wetland habitats may have direct benefits for some native amphibians and may also reduce the threat of exotic fish and bullfrogs, both of which were associated with permanent wetlands. Research and conservation efforts for lowland anurans in the West should emphasize the complexities of multiple contributing factors to amphibian losses.

JOURNAL OF WILDLIFE MANAGEMENT 63(4):1162–1171

Key words: amphibian declines, bullfrogs, exotic vertebrates, fish stocking, Puget Lowlands, *Rana aurora*, *Rana catesbeiana*, red-legged frogs, Washington, wetlands.

Losses of amphibian populations worldwide have received much recent attention (Blaustein and Wake 1990). Biologists have sought global explanations for declines, but research increasingly suggests multiple factors may be involved (Corn 1994). Attempts to explain amphibian declines are hampered by a lack of hypotheses consistent with global patterns and, at a local scale, by correlation among potential predictors. Exotic species and habitat change are considered leading threats to freshwater systems in the West (Richter et al. 1997) and may contribute to amphibian declines (Hayes and Jennings 1986, Corn 1994, Fisher and Shaffer 1996). With evidence that a concentration of apparent declines occurs in western North America (Wyman 1990, Corn 1994, Drost and Fellers 1996), the role of these factors merits further examination.

In western North America, the bullfrog and a variety of exotic fishes have been widely introduced for aquaculture and sport fishing (Jennings and Hayes 1985, Stebbins 1985, Moyle 1986). These exotics are suspect in some amphibian declines (Moyle 1973). An inverse association between bullfrogs and native anurans is quantified by 4 studies in California and Arizona (Moyle 1973, Hayes and Jennings 1988, Schwalbe and Rosen 1988, Fisher and Shaffer 1996), and numerous workers note that native anurans are rare in permanent wetlands inhabited by bullfrogs in the Pacific Northwest (Ja-

[1] Present address: U.S. Geological Survey Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331, USA.

[2] E-mail: mjadams@mail.cor.epa.gov

meson 1956, Green 1978, Nussbaum et al. 1983, Leonard et al. 1993). However, direct effects on the abundance of native amphibians are poorly quantified, and separating effects of bullfrogs from fish and habitat effects has proven difficult (Hayes and Jennings 1986, 1988).

Recent studies identified proximate mechanisms involving bullfrogs and exotic fishes that may result in native amphibian losses. Bullfrogs are large generalist predators capable of rapid population expansion (Bury and Whelan 1984), and they may affect native anurans by competition or predation (Kiesecker and Blaustein 1997, Kupferberg 1997, Lawler et al. 1999). Many of the fishes introduced in the West are efficient predators, and many amphibian larvae are poorly adapted to coexist with them (Kats et al. 1988, Werner and McPeek 1994, Skelly 1996, Tyler et al. 1998). Bullfrogs and exotic fishes are confined to permanent waters and may be more common in some altered habitats (Moyle 1973, Hayes and Jennings 1986, Kentula et al. 1992). The permanent wetlands most frequently occupied by exotics may systematically differ from unoccupied wetlands in their suitability for some native amphibians (Woodward 1983, Wellborn et al. 1996). Thus, hydrological or other habitat changes offer alternatives to the hypothesis that exotics are excluding some natives from permanent wetlands (Hayes and Jennings 1986).

The Puget Lowlands of Washington State (defined by Omernik [1987], also in Olson and Leonard [1997]) contain numerous and diverse wetlands. Bullfrogs, exotic fishes, and native anurans are all found in many wetland habitats (Adams et al. 1998, 1999). I used multivariate comparisons of bullfrog, fish, and habitat associations with red-legged frog occurrence at 2 spatial scales to examine the current distribution of red-legged frogs in the Puget Lowlands. Red-legged frogs are not officially considered threatened in Washington, but the presence of bullfrogs and the rarity of native frogs in permanent wetlands have long been used to infer that declines have occurred (e.g., Jameson 1956).

STUDY AREA

I conducted my study primarily on the Fort Lewis Military Reservation (34,400 ha) located at the southern tip of Puget Sound. Fort Lewis includes (1) part of the Nisqually River; (2) a number of large permanent lakes, ponds, and marshes; (3) many small temporary marshes; and (4) scattered seeps and springs. I refer to all lentic habitats as wetlands. Some wetlands on Fort Lewis had physical disturbances common to the Puget Lowlands (i.e., damming and dredging), but many were relatively undisturbed. I also sampled wetlands on the Submarine Base Bangor located on the west side of the Kitsap Peninsula bordering Hood Canal (approx 60 km north of Fort Lewis). Bangor is smaller than Fort Lewis (2,800 ha) but contains a variety of wetlands with vegetation and structure similar to Fort Lewis.

Detailed descriptions and maps of the habitats and species distributions on Fort Lewis and Bangor are in Adams et al. (1998, 1999). Bullfrogs, exotic fishes, red-legged frogs, and habitat characteristics were well distributed between and within the 2 study areas. Thus, there were no obvious geographic restrictions that could affect results. Study sites were spread over the bases, but the habitat-scale sampling was confined to Fort Lewis.

METHODS

I examined red-legged frog occurrence patterns at 2 spatial scales: habitat and wetland. The habitat scale analysis compared variables among independent, 125-m^2 plots in 17 wetlands. These plots (hereafter, habitat sites) had relatively homogenous vegetation (i.e., they did not include edges of vegetative associations) and had maximum depths ranging from 20 to 70 cm. The wetland-scale analysis used whole wetland traits determined from surveys of multiple subportions of wetlands. These subportions included, but were not limited to, the habitat-scale sites.

Habitat Scale

I selected habitat sites in 17 Fort Lewis wetlands for quantitative analysis. The habitat sites represented the full range of red-legged frog abundance based on amphibian surveys conducted in 1992 and 1993 (Adams et al. 1998). All habitat sites with abundant red-legged frogs were used, but sites with few or no red-legged frogs were randomly chosen. I only used wetlands where water persisted long enough for red-legged frog metamorphosis. I sampled 1 habitat site at most wetlands, but in 1996 I randomly chose 5 habitat sites from each of 3 of the larger wetlands (Chambers Lake [28 ha]; Johnson Marsh [80 ha]; Hardhack Marsh [52 ha]). The habitat sites were all at least 100 m apart, and I consider them independent. I used 15 habitat sites in 1994–95 and 24 sites in 1996 (n = 29 unique sites). This combination of random and deliberate site selection assured a wide range of red-legged frog population sizes, but any nonrandom sampling allows the possible introduction of bias. I averaged data over years because repeated-measures analysis of variance (ANOVA) did not reveal differences among years in red-legged frog capture rates at 14 habitat sites that were sampled each year ($F_{2,26}$ = 0.757, P = 0.479).

Red-legged frogs oviposit in early March, and larvae typically began metamorphosis in late July on Fort Lewis. I used wire minnow traps (19 cm diameter) to assess the relative abundance of red-legged frogs and the presence of bullfrogs and exotic fishes (Adams et al. 1997). I set 5 unbaited traps (4 in 1994) evenly over each habitat site and left them overnight (approx 15 hr) once in mid-June and once in early July of 1994 and 1995. In 1996, I could not complete the second trap period because military activities limited my access to Fort Lewis. I trapped 4–5 sites/night so that all sites could be trapped in 4–6 days. To reduce trap bias, I placed traps on the substrate and avoided structural irregularities. I used the mean number of captures per trapnight as an index of red-legged frog abundance.

Bullfrogs have a 1–2-year larval period in western Washington (Nussbaum et al. 1983) and older larvae are detectable by minnow traps, but capture rates dropped off as water temperatures rose. I also assessed bullfrog presence from call surveys and by listening for juvenile bullfrogs that "yelp" and flee when approached on foot (Nussbaum et al. 1983). This yelping behavior helped ensure that the frogs were equally detectable among sites, despite visibility differences. I conducted yelp counts 4–8 times at each site from June to August and used the average number of yelps per count as a measure of relative abundance for an analysis that only used sites where exotics were present.

I used minnow trap data to assess the presence of exotic fishes and supplemented those data in 1994 by trapping with 0.6-m-diameter funnel traps fitted with 2 5-m leads that helped funnel fish into the trap. I baited these large funnel traps with sardines or cat food. I did not use large funnel traps in subsequent years, because they caught less than the minnow traps and did not detect additional species.

I examined 9 habitat variables at the habitat scale (Table 1). I only measured and analyzed variables related to water temperature and native predators (salamanders, invertebrates) at a subset of 15 habitat sites.

Wetland Scale

I surveyed 26 Fort Lewis wetlands (1992–96) and 12 Bangor wetlands (1995, 1996) to assess red-legged frog occurrence patterns at the wetland scale. Some wetlands were connected for part of the year by streams or flooding events, but I considered all to be reasonably independent water bodies. I used a combination of funnel trapping, visual encounters, egg-mass searches, and call surveys to record presence of red-legged frogs, bullfrogs, and exotic fishes (for details see Adams et al. 1998, 1999). Due to their large size and problems with access, not all wetlands were surveyed in their entirety. Instead, I surveyed all wetlands at 3 or more subportions by using at least funnel trapping or egg mass surveys at each subportion. The subportions surveyed were all at least 125 m^2. Refraining from surveying whole wetlands allowed me to include some large wetlands but may have overlooked some populations inhabiting restricted portions of wetlands. By combining results of multiple surveys within wetlands, this analysis provided a means of examining patterns at a larger spatial scale. I surveyed 5 small wetlands (<0.5 ha) in their entirety. Habitat variables analyzed at the wetland scale were permanence and extent of emergent vegetation (Table 1).

Analysis

I used GLIM 4.0 (Francis et al. 1993) to conduct analysis of deviance (ANODEV) with forward selection to determine the best model predicting red-legged frog presence (wetland scale) and relative abundance (habitat scale). Binomial error with a logit link (logistic regression) was used to analyze presence, and Poisson error with a log link (Poisson regression) was used to analyze relative abundance (Aitkin et al. 1989). Poisson error was used for relative abundance data because of the frequency of zeros. An ANODEV is equivalent to an ANOVA for normal error but uses maximum likelihood rather than least-square estimation, and thus can accommodate other error distributions (Mc-

Table 1. Descriptions of habitat variables examined at wetlands surveyed on the Fort Lewis Military Reservation, 1992–96.

Variable	Description
Aspect[a]	Degrees deviation from a south aspect along a line perpendicular to shore. Most wetlands were lined with trees, and aspect relates to shading.
Slope[a]	Average slope of the substrate. Slope is related to the extent of emergent vegetation. Habitat sites with shallow slope had more extensive emergent vegetation.
Soft[a]	Is substrate consistency at site soft (Yes/No)? Soft = sink up to ankle or deeper. Tadpoles may use soft substrates for cover.
Phalaris[a]	Is reed canarygrass (*Phalaris arundinacea*) the dominant plant (Yes/No)? This plant was the only species of emergent vegetation that was dominant at >3 habitat sites.
Permanent[b]	Does the wetland dry (Yes/No)? Assessed from 1992 to 1996 and by questioning Fort Lewis environmental personnel.
Open[b]	Does <50% of the wetland's surface area have emergent vegetation (Yes/No)? Hayes and Jennings (1988) found emergent vegetation to correlate with red-legged frog distribution.
Distance[c]	Distance to the nearest wetland with a reproducing population of red-legged frogs. Immigration from nearby populations might obscure effects from exotics.
Temperature[d]	Water temperature and rate of warming in the spring were obtained from the intercept and slope of a linear regression of temperature on month. Thermometers recorded maximum and minimum temperatures monthly.
Invertebrates[d]	Relative abundance of predaceous invertebrates (combined dip-net sweeps of odonates, dytiscids, notonectids, and leeches) in April and June.
Salamanders[d]	Trap rate of salamanders (combined rate for rough-skinned newt [*Taricha granulosa*] and northwestern salamander [*Ambystoma gracile*]).

[a] Variables used at habitat scale.
[b] Variables used at whole wetland and mixed scales.
[c] Variable used in analysis of habitat-scale sites that had exotics.
[d] Variables used at a subset of 15 habitat-scale sites.

Cullagh and Nelder 1989). Link functions transform various nonlinear relations into linear relations (McCullagh and Nelder 1989:27).

Besides the habitat and wetland scale analyses, I conducted 2 post hoc analyses to determine if any other patterns could be detected. The first was at the habitat scale, but I only used habitat sites where exotics were present. I used ANODEV to compare the relative abundance of red-legged frog larvae to the relative abundance of bullfrogs (yelp counts), relative abundance of exotic fishes (mean number caught in minnow traps per trapnight), and the 2 habitat variables that were most significant from the other analyses. I also included distance to the nearest wetland with a reproducing population of red-legged frogs to determine if immigration might be obscuring effects of exotics. In my second post hoc analysis, I mixed scales and used ANODEV to examine the relation between relative abundance of red-legged frogs at the habitat scale and predictors at the wetland scale. I only used 1 site/wetland, which was randomly selected if I had sampled multiple sites via the habitat-scale protocol.

I used an F-test for most analyses to compensate for overdispersion and relatively low degrees of freedom (Smith 1991). However, the analysis that only includes sites where exotics were present was very underdispersed, and I used a chi-square test. I considered factors significant at $\alpha = 0.05$.

RESULTS

Habitat Scale

Red-legged frogs and bullfrogs were each present at 59% of the habitat sites, and 41% of habitat sites had exotic fishes. The distribution of bullfrogs was associated with the distribution of exotic fishes, but neither was associated with any habitat variables; thus, partitioning of exotic effects and habitat effects was possible at this scale (Table 2). The capture rate of red-legged frog larvae correlated with the number of juveniles found during timed searches, suggesting trap-rate may be a reasonably adequate index of abundance ($r_s = 0.80$, $P = 0.030$, $n = 8$).

Neither bullfrog nor exotic fish presence was related to the relative abundance of red-legged frogs at the habitat scale (Table 3). The best model included negative associations with slope and aspect. Red-legged frogs were most common at habitat sites with a shallow slope and

Table 2. Pearson correlation among predictors at habitat-scale study sites on the Fort Lewis Military Reservation, 1994–96 (n = 29 sites sampled).

	Fish	Aspect	Soft	Slope	Reed canarygrass
Bullfrogs	0.422*	−0.040	−0.147	−0.280	0.209
Fish		0.050	−0.017	0.098	0.224
Aspect			0.145	0.382*	−0.024
Soft				0.236	0.223
Slope					0.273

* $P < 0.05$.

southerly aspect (Fig. 1). Slope and aspect together explained 63% of the total deviance at the habitat scale, and neither bullfrogs nor exotic fishes were significant after they were entered into the model (Table 3, Fig. 1).

I obtained similar results by only examining habitat sites where exotics were found and by using relative abundance rather than presence of exotics as predictors (Table 4). Aspect, slope, and distance to the nearest site with red-legged frogs were the only habitat variables examined, and both aspect and slope were highly significant. Relative abundance of exotic fishes was also significant, but relative abundance of bullfrogs was not. Only aspect was significant in forward selection.

Relative abundance of red-legged frogs was not associated with temperature, predaceous invertebrates (early or late in the larval period), or salamanders (univariate ANODEV; all $Ps > 0.25$, df = 13) at a subset of habitat sites where I monitored temperature and native predators.

Wetland Scale

Associations between predictor variables resulted in partitioning difficulties (Table 5). However, there was no evidence that bullfrog presence was associated with the presence of red-legged frogs at wetlands. Red-legged frog presence was negatively associated with all other predictors. The best predictor of red-legged frog presence was the extent of open water (Fig. 2), and no other variable was significant after it was entered. Exotic fishes that were detected included sunfish (*Lepomis* spp.), yellow perch (*Perca flavescens*), smallmouth bass (*Micropterus dolomieui*), and 1 bullhead (*Ictalurus* sp.).

Mixed Scales

I found similar results when I compared relative abundance of red-legged frogs at the habitat scale to wetland-scale predictors. Bullfrog and exotic fish presence were not significant, but permanence and openness of water were (Table 6). The presence of exotic fishes was sig-

Table 3. Summary statistics for analysis of deviance of red-legged frog capture rate at the habitat scale on the Fort Lewis Military Reservation, 1994–96. Deviance (Dev) and F-values are cumulative for forward selection.

Source	df	Dev	F	P
Univariate regressions				
Total	28	63.709		
Bullfrog	1,27	2.813	1.247	0.274
Fish	1,27	7.364	3.529	0.071
Aspect	1,27	28.650	22.065	<0.001
Soft	1,27	0.300	0.128	0.723
Slope	1,27	34.800	32.499	<0.001
Phalaris	1,27	5.031	2.315	0.140
Forward selection				
Slope	1,27	34.800	32.499	<0.001
Aspect	1,26	5.869	6.622	0.016
Residual	26	22.613		
Not entered				
Bullfrog	1,25	2.214	2.713	0.116
Fish	1,25	0.479	0.541	0.473

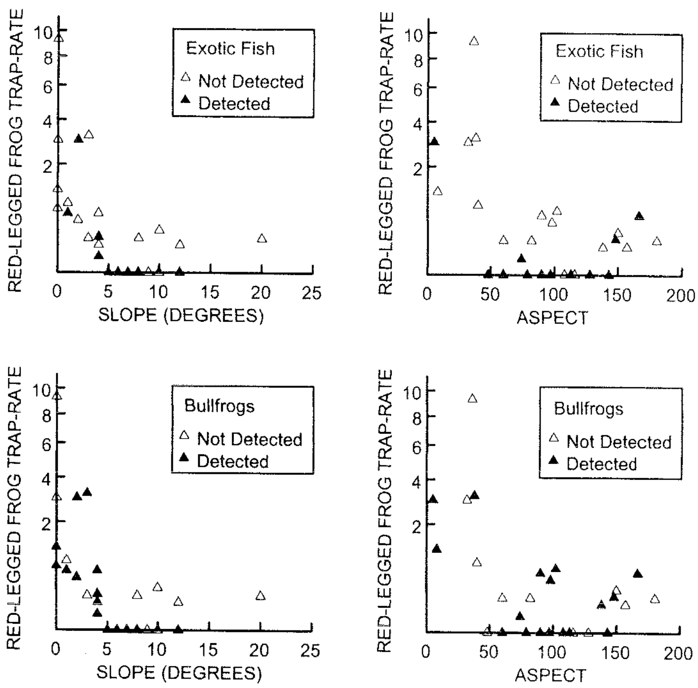

Fig. 1. The relative abundance of red-legged frogs on the Fort Lewis Military Reservation (1994–96) at the habitat scale in relation to bullfrogs, exotic fishes, slope, and aspect (degrees from south aspect). Trap rate is square-root transformed.

nificant after accounting for water permanence, but the association was positive; the interaction was not significant. Permanence alone explained 72% of the total deviance.

DISCUSSION

Amphibian declines may frequently be correlated with a suite of environmental changes.

Table 4. Summary statistics for analysis of deviance of red-legged frog capture rate at habitat scale only at sites on Fort Lewis where exotics were present, 1994–96. Deviance (Dev) is cumulative for forward selection.

Source	df	Dev	χ^2 (P)
Univariate regressions			
Total	17	22.156	
Bullfrog	1,16	0.001	0.977
Fish	1,16	4.792	0.029
Aspect	1,16	9.428	0.002
Slope	1,16	8.686	0.003
Distance	1,16	0.712	0.411
Forward selection			
Aspect	1,16	9.428	0.002
Residual	16	12.728	
Not entered			
Bullfrog	1,15	0.140	0.708
Fish	1,15	1.713	0.191
Slope	1,15	3.806	0.051
Distance	1,15	1.325	0.250

For example, drought, fish stocking, ultraviolet light, and a water mold (*Saprolegnia ferax*) may all be related to declines in some montane amphibian assemblages of western North America (Bradford 1989, Kiesecker and Blaustein 1995, Drost and Fellers 1996). Indirect effects, synergistic interactions, and regional differences in experimental results all complicate the search for causative agents (Corn 1994, Kiesecker and Blaustein 1995, Corn 1998, Kiesecker and Blaustein 1998). My findings emphasize the need for caution; the urgency of explaining declines must be tempered by the realization that interacting suites of environmental changes could produce complex effects that are difficult or inappropriate to isolate.

When bullfrogs are present, potential negative effects of habitat alterations and other exotic species are frequently overlooked. Because of their large size, high densities, and loud mating call, bullfrogs are a conspicuous disturbance to many permanent wetlands in the West (Bury and Whelan 1984). When native anurans are rare or absent from such sites, bullfrogs provide an obvious explanatory hypothesis. However, efforts to quantify the relation between bullfrogs and native anurans are hampered by the con-

Table 5. Association among wetland-scale variables on the Fort Lewis Military Reservation and Submarine Base Bangor, 1992–96. Table entries are *P*-values associated with likelihood-ratio chi-square tests. Sign indicates direction of association (n = 38 wetlands).

	Bullfrogs	Fish	Permanent	Open
Red-legged frog	0.500(−)	0.022(−)	0.050(−)	0.003(−)
Bullfrogs		<0.001(+)	0.005(+)	0.008(+)
Fish			0.008(+)	<0.001(+)
Permanent				<0.001(+)

founding influence of exotic fishes and habitat. In parts of California, where loss and alteration of wetland habitat has been extreme, there is almost complete overlap of bullfrogs, exotic fishes, and habitat alterations that may contribute to losses of native species (Moyle 1973, Hayes and Jennings 1988).

Overlap was less extreme in the Puget Lowlands, and my results do not support the hypothesis that bullfrogs are excluding red-legged frogs from wetlands. Negative associations between bullfrogs and red-legged frogs were weak or absent. A variety of analyses at different

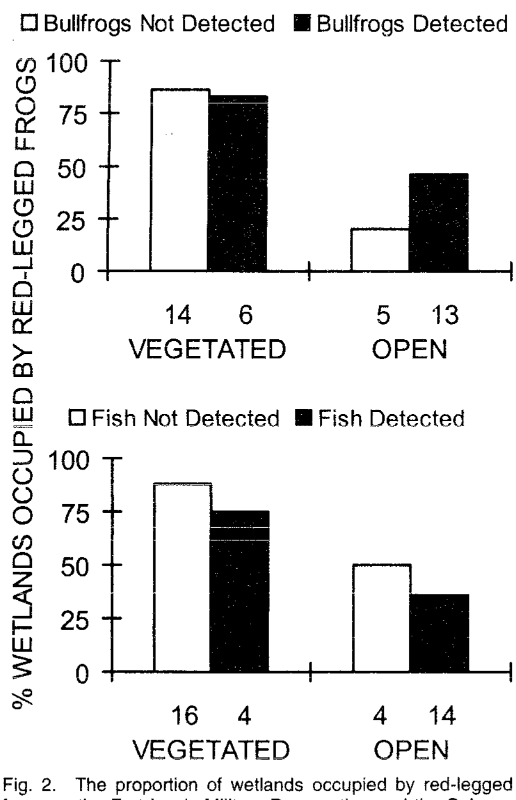

Fig. 2. The proportion of wetlands occupied by red-legged frogs on the Fort Lewis Military Reservation and the Submarine Base Bangor, 1992–96. Vegetated and open are defined in Table 1. Numbers below histograms are sample sizes for each category.

scales yielded consistently greater significance for exotic fishes than bullfrogs, suggesting that exotic fishes should be ranked a greater conservation concern than bullfrogs in the Puget Lowlands, if the sites I sampled are representative. Moreover, Richter and Azous (1995) and Adams et al. (1998) both failed to find a negative association between bullfrog presence and amphibian richness in Puget Lowland wetlands. Instead, they found that factors such as hydrology, vegetation complexity, and presence of exotic fishes were significantly associated with amphibian richness. Correlations between bullfrogs, exotic fishes, and habitat continue to pose analytical problems in the Puget Lowlands, but the diversity and abundance of wetlands and the availability of some permanent wetlands without exotics lessens the problem compared to studies in California. While bullfrogs appear widespread and abundant in the Puget Lowlands, an emerging question from these studies is whether the northern latitude lessens the effect of this warm-adapted species.

However, the introduction of a fecund, generalist predator like the bullfrog is always a threat to native ecosystems, and such exotics should likely be eradicated whenever possible. Indirect effects and potential interactions among bullfrogs, exotic fish, and habitat suggest these issues should not be treated independently. For example, Kiesecker and Blaustein (1998) found that the presence of bullfrog larvae increased the susceptibility of red-legged frog larvae to smallmouth bass predation in the Willamette Valley of Oregon. Also, there is evidence that fish can facilitate the persistence of bullfrogs in artificial ponds in Michigan (Werner and McPeek 1994).

Further, water permanence affects the distribution of exotics but may also have direct effects on some native amphibians and can be viewed as a primary organizing factor for aquatic communities (Wellborn et al. 1996). Water permanence affects potential predators and the

Table 6. Summary statistics for analysis of deviance comparing red-legged frog capture rate at the habitat scale to predictors at the wetland scale on the Fort Lewis Military Reservation, 1994–96. The association with fish was positive after permanence was entered in the model. All other associations were negative. Deviance (Dev) and *F*-values are cumulative for forward selection.

Source	df	Dev	*F*	*P*
Univariate regressions				
Total	15	92.254		
Bullfrogs	1,14	0.028	0.004	0.950
Fish	1,14	1.519	0.234	0.636
Permanent	1,14	66.610	36.321	<0.001
Open	1,14	32.210	7.507	0.016
Forward selection				
Permanent	1,14	66.610	36.321	<0.001
Fish	1,13	12.700	12.720	0.003
Residual	13	12.98		
Not entered				
Bullfrogs	1,12	1.098	1.109	0.313
Open	1,12	1.113	1.126	0.310

larval life-history strategy of anurans (e.g., Skelly 1995). It can also affect the productivity of wetlands (Gosselink and Turner 1978), which may in turn affect food availability and susceptibility of amphibian larvae to predators (e.g., Anholt and Werner 1995). Adams (1997) found that direct negative effects of exotic species were possible, but they were not responsible for the low survival of red-legged frog and Pacific treefrog (*Hyla regilla*) larvae in some permanent Puget Lowland ponds. Instead, habitat or indirect effects of exotics appeared to be important. Similarly, I found that habitat variables were the best predictors of red-legged frog occurrence at a regional scale (Figs. 1, 2).

By relying heavily on funnel-trapping data, I focused on red-legged frog larval (rather than adult) associations with exotic fishes and bullfrogs (particularly at the habitat scale where funnel traps were used exclusively). Predation by bullfrogs on postmetamorphic native anurans could have gone undetected if the effect of this predation did not carry over to subsequent breeding efforts. At sites near a source population of native anurans, immigrants could reproduce and replenish tadpole populations with few of the metamorphs surviving to return and breed (Sjögren 1991). However, the lack of correlation between red-legged frog abundance and distance to potential source populations (Table 5) suggests source–sink dynamics may not be occurring.

MANAGEMENT IMPLICATIONS

The prevalence of habitat changes merits concern in conservation efforts for the red-legged frog in the Puget Lowlands. A general trend in western North America is that human effects are altering hydrology and increasing the proportion of wetlands that have permanent standing water (Kentula et al. 1992, Richter et al. 1997). Permanent wetlands generally differ from temporary wetlands in productivity, native predator communities, vulnerability to exotics, and structural characteristics, and a variety of aquatic organisms are specialized to a narrow portion of the permanence gradient (Gosselink and Turner 1978, Woodward 1983, Holland et al. 1995, Wellborn et al. 1996). It is increasingly important that wetland mitigation and restoration efforts attempt to recreate temporary habitats that are being disproportionately lost (Kentula et al. 1992).

I do not suggest that permanent wetlands are without value for red-legged frogs or other wildlife. Rather, red-legged frogs were most abundant in seasonally flooded areas associated with permanent wetlands and in temporary wetlands that held standing water through at least late-July. This pattern suggests permanence itself is not the most important variable for red-legged frogs, but that the general loss of shallow, emergent marsh may be detrimental. Conserving broad, seasonally flooded areas associated with deeper, permanent waters may benefit red-legged frogs. Moreover, the practice of "enhancing" wetlands by dredging out more open water may be detrimental.

It is inappropriate to dismiss a potential effect of bullfrogs on red-legged frogs, even in the Puget Lowlands. My results only suggest bullfrogs may not be a major limiting factor for red-legged frogs at the regional scale in the Puget Lowlands. The lack of association between red-legged frogs and bullfrogs in this study is not evidence that no effect exists, nor that any existing effect is unimportant. Even the exclusion of red-legged frogs from a few habitats by bullfrogs could be ecologically important, but statistically insignificant. Moreover, patterns may differ in southern regions where bullfrogs may be more abundant.

To the degree that simple policy changes (such as removing bullfrog take-limits) might reduce bullfrog numbers or limit their spread, removal of bullfrogs is obviously justifiable. However, eradication of bullfrogs, even from individual wetlands, is likely to be costly if even possible (although creative new techniques might help; e.g., Wassersug 1997). Attempting bullfrog eradication to help native frogs at the regional scale is questionable given the available data and scarcity of funding, but such action may be advisable in some local situations. Instead, conservation of a diverse array of wetland habitats appears more likely to help native amphibians and may also serve to limit the distribution of exotics.

ACKNOWLEDGMENTS

The Fort Lewis Military Reservation, The Nature Conservancy, and the U.S. Naval Submarine Base Bangor supported this research. I thank J. K. Agee, K. B. Aubry, R. B. Bury, P. S. Corn, J. L. Erickson, R. Gitzen, J. M. Kiesecker, T. P. Quinn, J. R. Skalski, D. K. Skelly, and S. D. West for providing comments and discussion on design and earlier drafts of this manuscript. L. Hallock, W. P. Leonard, and S. A. Swarts provided field assistance, and I am especially grateful to S. Claeson for her long hours. A. B. Carey was instrumental in obtaining funding. Suggestions from C. A. Pearl and 2 anonymous reviewers improved this manuscript.

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Received 28 July 1998.
Accepted 15 April 1999.
Associate Editor: Lutz.