



## Research Article

# Non-Native Species Impacts on Pond Occupancy by an Anuran

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**ABSTRACT** Non-native fish and bullfrogs (*Lithobates catesbeianus*) are frequently cited as contributing to the decline of ranid frogs in the western United States, so we hypothesized that non-native species, habitat, or a combination of these relate to the probability of local extinction for northern red-legged frogs (*Rana aurora*) in Oregon, USA. We also hypothesized that the probability of colonization relates to land use, wetland size, or riparian forest. In a 5-yr study, we found no support for an effect of non-native species on northern red-legged frogs. Instead, probability of local extinction decreased with the extent of emergent vegetation and riparian forest. This finding suggests that managers consider the role of habitat when confronting non-native species problems. © 2011 The Wildlife Society.<sup>†</sup>

**KEY WORDS** bullfrogs, colonization, fish, local extinction, non-native species, northern red-legged frog, occupancy, *Rana aurora*, wetlands.

Non-native fish and bullfrogs (*Lithobates catesbeianus*; *Rana catesbeiana*) are frequently cited as factors contributing to the decline of ranid frogs in the western United States (Bradford 2005). This hypothesis is supported by studies showing competition with or predation by these introduced species (Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999, Knapp et al. 2001) and studies suggesting a deficit of native frogs at sites occupied by bullfrogs or game fish (Hammerson 1982, Schwalbe and Rosen 1988, Fisher and Shaffer 1996, Adams 1999). Conversely, other studies failed to find a negative association between native ranids and bullfrogs and point out that presence of non-native species correlates with habitat alterations that could also contribute to declines of native species (Hayes and Jennings 1986; Adams 1999, 2000; Pearl et al. 2005). A criticism of these studies is that they may not detect an effect of non-native species if the process of displacement is at an early stage. We are not aware of any studies that have monitored a set of native frog populations to determine if non-native species predict population losses. Our objective was to study site occupancy trends in relation to non-native species for northern red-legged frogs (*Rana aurora*) on federal lands in the southern Willamette Valley, Oregon.

We conducted a 5-yr monitoring study to answer the following questions about the status and trends of the northern red-legged frog: 1) What is the rate of local extinction (how often is a site that is occupied in year  $t$  unoccupied in year  $t + 1$ ) and what factors predict variation in local extinction? and 2) What is the rate of colonization (how often is a

site that is unoccupied in year  $t$  occupied in year  $t + 1$ ) and what factors predict variation in colonization? The factors we hypothesized for local extinction were: 1) bullfrog presence, 2) bullfrogs mediated by wetland vegetation, 3) non-native fish (Centrarchidae), 4) non-native fish mediated by wetland vegetation, 5) extent of emergent vegetation, 6) extent of riparian forest, and 7) a combined effect of bullfrogs and fish. The factors that we hypothesized for colonization were: 1) the extent of human influence in the surrounding landscape, 2) riparian forest, and 3) wetland size.

## STUDY AREA

The Willamette Valley is a broad agricultural valley that drains the Coast and Cascade Mountain Ranges in western Oregon, USA. The largest urban areas (Portland and Eugene) were at the north and south ends of the valley. Two ranid frogs were native there: the Oregon spotted frog (*Rana pretiosa*) was thought to be extirpated from the Valley and the northern red-legged frog was thought to be declining. Habitat loss and alteration were substantial and appeared to explain much of the declines in northern red-legged frogs (Kentula et al. 1992, Adams et al. 1998, Adams 1999, Pearl et al. 2005), but introduced fish and bullfrogs continue to be cited as factors in the declines of both species (Kiesecker 2003). There was some evidence that the Oregon spotted frog may be more susceptible to bullfrog predation than the northern red-legged frog which may explain why the 2 species have fared differently despite using similar breeding habitats (Pearl et al. 2004). There was also evidence that non-native fish may exacerbate the bullfrog problem (Adams et al. 2003) and that bullfrog presence can increase predation by smallmouth bass (*Micropterus dolomieu*) on northern red-legged frog tadpoles (Kiesecker and Blaustein 1998).

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Our study area was on the U. S. Fish and Wildlife Service, Willamette Valley Refuge Complex which included Finley, Ankeny, and Baskett Slough National Wildlife Refuges. We also had 3 sites on the Bureau of Land Management, West Eugene Wetlands Complex in the southern Willamette Valley. A variety of habitat management occurred on these lands (typically for waterfowl) but, unlike the rest of the Willamette Valley, wetland loss was minimal. Our range of inference was to all lentic habitats that we considered likely to persist through June in most years ( $N = 69$ ). We based our assessment of hydroperiod on personal experience and conversations with land managers. There is no published information on population or occupancy trends in northern red-legged frogs within our study area.

## METHODS

We randomly chose 42 wetlands to monitor but concluded with a sample size of 39 after excluding 3 wetlands that consistently failed to maintain sufficient surface water for amphibian reproduction. For wetlands  $>1$  ha, we chose a subset of the wetland to monitor. We chose an area  $<1$  ha that was accessible and had extensive littoral habitats. Beginning in spring of 2004, we sampled wetlands by placing 10 collapsible minnow traps with 5.8-cm openings on the substrate in shallow areas where the top of the trap would protrude above the water. We spread traps evenly throughout the monitoring area. We set traps after noon and removed them the following morning. Beginning in 2006, we set traps on an additional night 1–3 weeks after the first sampling date at a subset of 10 randomly chosen wetlands that changed each year. We used 10 traps/site for the second effort in 2006 and 5 traps/site for the second visit in subsequent years. We placed traps in the second visit without regard to previous placements. We sampled from late-April when larvae were large enough to trap to mid-June when metamorphosis for some species began. We considered red-legged frogs present if we detected larvae but, in practice, we never trapped adults or juveniles without also catching larvae. Sampling procedures were approved by the Oregon State University, Office of Research Integrity (IACUC3406) and permitted annually by the Oregon Department of Fish and Wildlife.

We designed our sampling to provide data suitable for an occupancy analysis (MacKenzie et al. 2006). Occupancy models use repeat observations to estimate probability ( $P$ ) that one observation will detect a species that is present. We treated trap nights as observations, so we treated 10 traps at a site as 10 observations, similar to design option 4 by MacKenzie et al. (2006:162) that substitutes spatial replicates for temporal replicates. Occupancy models allow an estimate of the probability ( $\psi$ ) that a site is occupied and they can be used to examine the relationship between  $\psi$  and site characteristics. We used a multi-season occupancy model that also estimates the probability that an unoccupied site will be colonized ( $\gamma$ ) and the probability that an occupied site will suffer a local extinction ( $\epsilon$ ; MacKenzie et al. 2003). We used the parameterization of the multi-season occupancy model that directly estimates initial occupancy (i.e.,  $\psi$  in season 1) but not  $\psi$  in subsequent seasons.

There are 2 types of covariate in occupancy models: observation and site. Observation covariates can have different values for each individual observation. In our study, the individual observations equated with trap nights. We used the total number of minutes a trap was set (Time), average of the water temperatures at the time we set a trap and the time we removed it (WT), and number of days since 1 January to the day we set a trap (Date) as observation covariates to account for the effect of these factors on probability of detecting red-legged frog larvae when they were present.

Site covariates had one value for each wetland and did not vary among observations. Each year, we visually estimated percent of the shoreline that had trees taller than 5 m within 5 m of the bank and percent of the wetland that had emergent vegetation. We averaged these percentages across years to calculate the variables Forest and Veg, respectively. Emergent vegetation has repeatedly been shown to relate to red-legged frog occupancy in the Pacific Northwest (Adams et al. 1998, Adams 1999, Pearl et al. 2005). We hypothesized an effect of riparian trees based on anecdotal observations. We noted if maximum depth of the wetland during high water appeared to be  $>2$  m. This classification was usually obvious and there was seldom disagreement among years, but we used the most frequently recorded value as the variable Depth, which has been shown to relate to red-legged frog occupancy in previous work (Pearl et al. 2005). We used the average trap rate of bullfrogs across all years for each site as an index of bullfrog abundance (Bull). The variable Fyrs was the total number of years that we detected non-native fish (Centrarchidae). We used Fyrs instead of fish presence (Fish) in our a priori analysis because we think Fyrs served as a crude index of abundance and perhaps of the persistence of fish at each site. In either case, a higher number should indicate more opportunity for an effect of fish on northern red-legged frogs. We did not record the number of fish/trap in the first years of the study so we could not calculate trap rate. We determined Area ( $m^2$ ) for each wetland by tracing polygons from aerial images accessed on Google Earth<sup>TM</sup> (<http://earth.google.com>) on 26 March 2009. The images were dated 29 June 2005 for most of the sites and 3 September 2006 for 3 wetlands on lands administered by the Bureau of Land Management. We hypothesized that larger sites might be more likely to be colonized. Finally, we calculated an index of human activity (HF) by averaging the values from the index called Human Footprint developed by Leu et al. (2008) for a 500-m buffer around each wetland. We hypothesized that human activities may affect the ability of red-legged frogs to move through the landscape and colonize new sites. We standardized all continuous covariates to  $\bar{x} = 0$  and  $SD = 1$ .

We began the analysis by examining the Pearson correlation among the covariates described above. We retained all covariates (all  $R \leq 0.7$ ). We then fit a global model with the following structure:  $\psi_1(\text{Forest, Veg, Depth, Fyrs})$ ,  $\gamma(\text{HF, Area, Forest})$ ,  $\epsilon(\text{Bull, Fyrs, Veg, Forest, Veg} \times \text{Bull, Veg} \times \text{Fyrs})$ ,  $P(\text{Time, Date, WT, Forest, Veg, Depth, Bull, Fyrs})$ . Each parameter is a logit function of the covariates shown in parentheses. We chose the covariates of  $\psi_1$

**Table 1.** Model comparison for hypotheses concerning the probability of local extinction for northern red-legged frogs on federal lands in the Willamette Valley, Oregon, USA, 2004–2008. Each model is a variation of the global model ( $\psi_1$ [Forest, Veg, Depth, Fyrs],  $\gamma$ [HF, Area, Forest],  $\epsilon$ [Bull, Fyrs, Veg, Forest, Veg  $\times$  Bull, Veg  $\times$  Fyrs],  $P$ [Time, Date, WT, Forest, Veg, Depth, Bull, Fyrs]) where  $\psi_1$  = probability of occupancy in year 1, Forest = % of wetland with riparian trees, Veg = % of wetland with emergent vegetation, Depth = 1 if maximum water depth >2 m or 0 if not, Fyrs = number of years non-native fish were detected,  $\gamma$  = probability of colonization, HF = human footprint score, Area = area of wetland (m<sup>2</sup>),  $\epsilon$  = probability of extinction, Bull = mean trap rate of bullfrogs,  $P$  = probability of detection, Time = total minutes trap was set, Date = days since 1 January of current year, and WT = mean water temperature (C). Only the extinction function ( $\epsilon$ ) differs among models.

Model	AIC <sub>c</sub> <sup>a</sup>	$\Delta$ AIC <sub>c</sub> <sup>b</sup>	$w^c$	Model likelihood	No. parameters	(-2 $\times$ LogLike)
Global, $\epsilon$ (forest, veg)	1315.53	0.00	0.870	1.000	21	1273.53
Global, $\epsilon$ (global)	1321.37	5.84	0.047	0.054	25	1271.37
Global, $\epsilon$ (forest)	1322.20	6.67	0.031	0.036	20	1282.20
Global, $\epsilon$ (.)	1323.33	7.80	0.018	0.020	19	1285.33
Global, $\epsilon$ (veg)	1323.90	8.37	0.013	0.015	20	1283.90
Global, $\epsilon$ (Fyrs)	1325.20	9.67	0.007	0.008	20	1285.20
Global, $\epsilon$ (bull)	1325.27	9.74	0.007	0.008	20	1285.27
Global, $\epsilon$ (bull $\times$ veg)	1326.19	10.66	0.004	0.005	22	1282.19
Global, $\epsilon$ (Fyrs $\times$ veg)	1327.10	11.57	0.003	0.003	22	1283.10
Global, $\epsilon$ (Fyrs $\times$ bull)	1328.97	13.44	0.001	0.001	22	1284.97
$\psi$ (.), $\gamma$ (.), $\epsilon$ (.), $P$ (.)	1333.53	18.00	0.000	0.000	4	1325.53

<sup>a</sup> Akaike's Information Criterion for small sample sizes.

<sup>b</sup>  $\Delta$ AIC<sub>c</sub> for the current model minus the minimum  $\Delta$ AIC<sub>c</sub>.

<sup>c</sup> Akaike's weight.

based on findings of previous studies in the Pacific Northwest (Adams 1999, Pearl et al. 2005) and included all covariates of  $\psi_1$  and  $\epsilon$  as covariates of  $P$  to account for any heterogeneity in detection probability that might bias estimates of those parameters. We included the interactions Veg  $\times$  Bull and Veg  $\times$  Fyrs because we hypothesized that extensive vegetation may reduce any negative effects of fish and bullfrogs (Adams et al. 1998, Adams 1999). We used the software PRESENCE (Version 2.2, [www.mbr-pwrc.usgs.gov/software/](http://www.mbr-pwrc.usgs.gov/software/), accessed 15 Mar 2009) to maximize the joint likelihood of the estimates given the data. Although the global model is almost certainly over-parameterized, we determined that it was not excessively so by dropping each covariate individually and comparing the AIC<sub>c</sub> (Akaike's Information Criterion for small samples) of the reduced model to the global model. An improvement >2 AIC<sub>c</sub> units as a result of dropping a covariate might indicate it is inappropriate and its influence might warrant further examination. We found no such improvements.

Next, we fit a series of models to represent our hypotheses concerning extinction and colonization and used AIC<sub>c</sub> to

rank these models. Each model differed from the global model in the formulation of one component ( $\gamma$  or  $\epsilon$ ) and only included the covariates of that component that related to one of our hypotheses. For example, the model representing our hypothesis that bullfrog presence relates to probability of local extinction only included Bull as a covariate of  $\epsilon$  and used the global model for all other components ( $\psi_1$ ,  $\gamma$ , and  $P$ ; Table 1). Likewise, the model representing our hypothesis that riparian forest relates to probability of colonization only included Forest as a covariate of  $\gamma$  and used the global model for all other components ( $\psi_1$ ,  $\epsilon$ , and  $P$ ; Table 2). We based conclusions on the ranking of the models and on estimates of the effects of covariates on the parameters in the model. Based on the ranking of our hypothesized models, we investigated the support for some additional variations on the global model including the effect of using a simple detected-not detected covariate for fish instead of the number of years we detected fish and the effect of forest within 500 m of a wetland on  $\epsilon$ . We also investigated whether the best model could be improved by allowing annual variation in  $\epsilon$ . We report an estimate of occupancy in season 1 ( $\psi_1$ ) from the

**Table 2.** Model comparison for hypotheses concerning colonization for northern red-legged frogs on federal lands in the Willamette Valley, Oregon, USA, 2004–2008. Each model is a variation of the global model ( $\psi_1$ [Forest, Veg, Depth, Fyrs],  $\gamma$ [HF, Area, Forest],  $\epsilon$ [Bull, Fyrs, Veg, Forest, Veg  $\times$  Bull, Veg  $\times$  Fyrs],  $P$ [Time, Date, WT, Forest, Veg, Depth, Bull, Fyrs]) where  $\psi_1$  = probability of occupancy in year 1, Forest = % of wetland with riparian trees, Veg = % of wetland with emergent vegetation, Depth = 1 if maximum water depth >2 m or 0 if not, Fyrs = number of years non-native fish were detected,  $\gamma$  = probability of colonization, HF = human footprint score, Area = area of wetland (m<sup>2</sup>),  $\epsilon$  = probability of extinction, Bull = mean trap rate of bullfrogs,  $P$  = probability of detection, Time = total minutes trap was set, Date = days since 1 January of current year, and WT = mean water temperature (C). Only the colonization function ( $\gamma$ ) differs among models.

Model	AIC <sub>c</sub> <sup>a</sup>	$\Delta$ AIC <sub>c</sub> <sup>b</sup>	$w^c$	Model likelihood	No. parameters	(-2 $\times$ LogLike)
Global, $\gamma$ (.)	1318.15	0	0.343	1.000	22	1274.15
Global, $\gamma$ (forest)	1318.76	0.61	0.253	0.737	23	1272.76
Global, $\gamma$ (HF500)	1319.44	1.29	0.180	0.525	23	1273.44
Global, $\gamma$ (area)	1319.74	1.59	0.155	0.452	23	1273.74
Global, $\gamma$ (global)	1321.37	3.22	0.069	0.200	25	1271.37
$\psi$ (.), $\gamma$ (.), $\epsilon$ (.), $P$ (.)	1333.53	15.38	0.000	0.001	4	1325.53

<sup>a</sup> Akaike's Information Criterion for small sample sizes.

<sup>b</sup>  $\Delta$ AIC<sub>c</sub> for the current model minus the minimum  $\Delta$ AIC<sub>c</sub>.

<sup>c</sup> Akaike's weight.

global model modified to allow extinction and colonization to vary among years. We used the same model to derive values for  $\psi$  in subsequent seasons that are based on the estimated model parameters (MacKenzie et al. 2003).

The use of occupancy models requires the assumption that there is no unexplained heterogeneity in  $P$ . We used the goodness-of-fit test available in PRESENCE to test this assumption (MacKenzie and Bailey 2004). The test is only available for the single season model so we used the 2004 data to fit  $\psi$ (Forest, Veg, Depth, Fyrs),  $P$ (Time, Date, WT, Forest, Veg, Depth, Bull, Fyrs) with 10,000 parametric bootstraps.

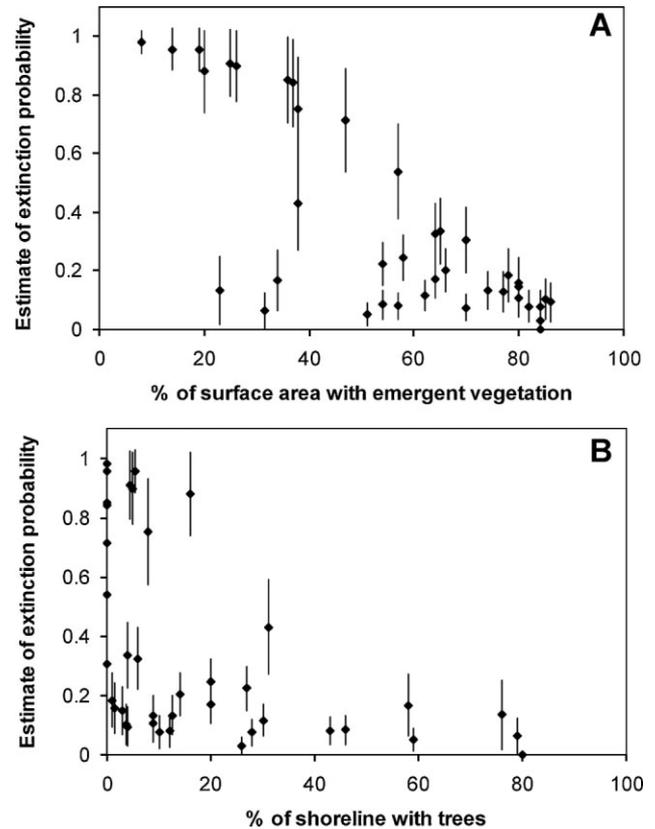
## RESULTS

We detected northern red-legged frogs at 15 of 39 sites (0.38) in the first year of our study. The average of individual site estimates of the probability of occupancy in year 1 was  $\psi_1 = 0.42$  ( $n = 39$ , range  $\hat{\psi} = 0.05$ – $0.76$ , average SE = 0.166). Means of derived site estimates of  $\psi$  for subsequent years were  $\psi_2 = 0.41$ ,  $\psi_3 = 0.43$ ,  $\psi_4 = 0.43$ , and  $\psi_5 = 0.41$ . In 17 instances we did not detect northern red-legged frogs at a site where they were found in the previous year and in 13 instances we detected them at a site where they were not seen in the previous year.

We found little support for any of the models involving introduced species as covariates of  $\varepsilon$ . Not only were these the lowest ranked hypothesized models, but they were also worse than the model with no covariates of  $\varepsilon$  (Table 1). Instead, our analysis favored the hypothesis that both aquatic and riparian vegetation were associated with  $\varepsilon$  over all other hypotheses (Fig. 1). This model estimated that the odds of local extinction decreased by a factor of 0.547 (95% CI = 0.354–0.845) for every 10% of shoreline with trees and by a factor of 0.469 (95% CI = 0.256–0.864) for every 10% of surface area that had emergent vegetation.

A post hoc model that allowed annual variation in  $\varepsilon$  did not improve the model but had weak support ( $w = 0.20$ ). A variation on the global model that replaced Fyrs with Fish Presence was not supported ( $w = 0.01$ ). Because the variable Forest only considered trees within 5 m of shore, we tried replacing Forest with percentage forest cover within a 500-m buffer around the wetland site we monitored. This change was not supported ( $w = 0.00$ ). A goodness-of-fit test using the 2004 data did not suggest presence of any unexplained heterogeneity ( $P = 0.485$ ,  $\hat{c} = 1.004$ ).

Whereas all of the a priori models for colonization (except the global model) had  $\Delta AIC_c < 2.0$ , the best model had no covariates (Table 2). The effect of all 3 covariates trended positive but 95% confidence intervals did not exclude 1 (no effect) for any effect, which gives little support for any covariates of colonization but does not conclusively rule them out. A post hoc model that allowed colonization to vary among years but not among sites was the worst colonization model we examined ( $w = 0.03$ ), and a model that allowed both extinction and colonization to vary among years was the worst of all the models we examined ( $w = 0.00$ ). Thus, we did not allow annual variation and estimated that probability of any unoccupied pond in our study being colonized during any year was  $\hat{\gamma} = 0.168$  (95% CI = 0.100–0.268).



**Figure 1.** The relationship of the probability of local extinction with wetland (A) and riparian vegetation (B) for northern red-legged frogs on federal lands in the Willamette Valley, Oregon, 2004–2008. Data points are estimates based on the top-ranked occupancy model. Vertical bars are SE of the estimate.

## DISCUSSION

Although there is ample reason to be concerned that habitat loss and alteration have negative consequences for northern red-legged frogs in the Willamette Valley, we found no evidence of declines in occupancy from 2004 to 2008 on federal lands where habitats are relatively intact compared to most other lands in the Willamette Valley. Instead, local extinctions appeared to be offset by colonization of unoccupied wetlands such that the occupancy rate was approximately stable. This pattern occurred despite the detection of non-native centrarchids at 72% of the wetlands, and bullfrogs at 74% of the wetlands, we monitored. There was already evidence that northern red-legged frogs do not have a negative association with bullfrogs in the Pacific Northwest (Richter and Azous 1995, Adams et al. 1998, Adams 1999, Pearl et al. 2005) but these same studies each found a negative association with centrarchids. Moreover, there is experimental evidence of negative effects of pumpkinseed (*Lepomis gibbosus*) and smallmouth bass on northern red-legged frogs via predation on tadpoles (Kiesecker and Blaustein 1998, Adams 2000). We stress that the lack of an association between non-native species and  $\varepsilon$  in our study does not mean that no negative effects occur. Five years is a short time period to use local extinctions to assess the consequences of non-native species. We continue to

monitor amphibians at these wetlands as part of the United States Geological Survey's Amphibian Research and Monitoring Initiative (Corn et al. 2005).

Our results are encouraging in that they suggest that habitat conditions may play a role in the persistence of northern red-legged frogs despite presence of non-native fish and bullfrogs. That wetland vegetation is related to the probability of local extinction is consistent with previous work that found an association of northern red-legged frogs or amphibian richness with wetland vegetation that was stronger than associations with non-native fish (Richter and Azous 1995, Adams et al. 1998, Adams 1999, Pearl et al. 2005). We are not aware of previous studies documenting the importance of riparian vegetation for northern red-legged frogs, but it is consistent with their relatively terrestrial nature compared to some other ranids. Upland vegetation has proven important for other ranids with similar natural histories (Semlitsch and Bodie 2003), and one study suggests that northern red-legged frogs prefer to move through forest rather than clearcuts (Chan-McLeod 2003). Our results are also consistent with the recommendations of Adams and Pearl (2007) that the best way to manage the bullfrog problem in some areas may be an indirect approach that focuses on habitat rather than direct control of bullfrogs.

Occupancy models are a tool to reduce bias caused by false negatives in detected-not detected data. Such data can underestimate occupancy probabilities and overestimate local extinction and colonization probabilities. The ability of occupancy models to reduce bias hinges on design-based or model-based reduction of heterogeneity in detection probability (MacKenzie et al. 2002). We included all covariates of occupancy and extinction as covariates of detection probability to ensure that any heterogeneity in detection probability did not bias the other parameter estimates with respect to our hypotheses.

Our design differed somewhat from a conventional occupancy approach in that the repeated observations were traps. For example, we treated 10 traps in a wetland as 10 observations. Our approach relies on the assumption that catching animals in one trap does not affect the trap rate of other traps. To some extent, this assumption must be false because a captured animal cannot be caught in another trap. We assume this effect is vanishingly small because capture probabilities using traps are thought to be very low and we set traps >5 m apart. Our approach also relies on the assumption that, if northern red-legged frogs are caught in  $\geq 1$  trap at a site, then any trap at that site has some chance of detecting northern red-legged frogs. This assumption is difficult to assess but our observation is that this species tends to be widely distributed around a site rather than clustered in a small area. Simulations suggest that this bias is mitigated if the sampling fraction of possible locations is very small (Kendall and White 2009). We believe this is the case in our study because the traps sample a very small area and the opportunities for trap placement can be seen as infinite.

We note that the multi-season occupancy model we used adjusted for bias in the detection of red-legged frogs but not

of bullfrogs or non-native fish. We interpreted the variables Bull and Fyrs as if they reflected variation in abundance or occupancy, but we recognize that they also contain an unknown amount of heterogeneity attributable to capture probability or detection probability. A multi-species occupancy model exists to estimate and accommodate detection probability issues for multiple species simultaneously but only for 1 yr (MacKenzie et al. 2004).

## MANAGEMENT IMPLICATIONS

Our study suggests the possibility that habitat characteristics of wetlands could be used to promote the persistence of northern red-legged frog populations despite the presence of bullfrogs and non-native fish. Wetlands with >35% of their perimeter with trees had the lowest probabilities of local extinction ( $\hat{\epsilon} < 0.2$ ). Also, wetlands that had >60% of their surface area with emergent vegetation had  $\hat{\epsilon} < 0.4$ . There remains reason to be concerned about non-native fish and bullfrogs but our study does not show evidence of negative effects.

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## 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.
- Adams, M. J. 2000. Pond permanence and the effects of exotic vertebrates on anurans. *Ecological Applications* 10:559–568.
- Adams, M. J., R. B. Bury, and S. A. Swarts. 1998. Amphibians of the Fort Lewis Military Reservation, Washington: sampling techniques and community patterns. *Northwestern Naturalist* 79:12–18.
- Adams, M. J., and C. A. Pearl. 2007. Problems and opportunities managing invasive bullfrogs: is there any hope? Pages 679–693 in F. Gherardi, editor. *Biological invaders in inland waters: profiles, distribution and threats*. Springer, Dordrecht, The Netherlands.
- Adams, M. J., C. A. Pearl, and R. B. Bury. 2003. Indirect facilitation of an anuran invasion by non-native fishes. *Ecology Letters* 6:343–351.
- Bradford, D. F. 2005. Factors implicated in amphibian population declines in the United States. Pages 915–925 in M. Lannoo, editor. *Amphibian declines: the conservation status of United States species*. University of California, Berkeley, USA.
- Chan-McLeod, A. C. A. 2003. Factors affecting the permeability of clearcuts to red-legged frogs. *Journal of Wildlife Management* 67:663–671.
- Corn, P. S., E. Muths, M. J. Adams, and C. K. Dodd, Jr., 2005. The United States Geological Survey's Amphibian Research and Monitoring Initiative. *Alytes* 22:65–71.
- Fisher, R. N., and H. B. Shaffer. 1996. The decline of amphibians in California's great central valley. *Conservation Biology* 10:1387–1397.
- Hammerson, G. A. 1982. Bullfrog eliminating leopard frogs in Colorado? *Herpetological Review* 13:115–116.
- 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.
- Kendall, W. L., and G. C. White. 2009. A cautionary note on substituting spatial subunits for repeated temporal sampling in studies of site occupancy. *Journal of Applied Ecology* 46:1182–1188.

- 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. 2003. Invasive species as a global problem: toward understanding the worldwide decline of amphibians. Pages 113–126 in R. D. Semlitsch, editor. *Amphibian conservation*. Smithsonian Institution, Washington, District of Columbia, USA.
- 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.
- Knapp, R. A., K. R. Matthews, and O. Sarnelle. 2001. Resistance and resilience of alpine lake fauna to fish introductions. *Ecological Monographs* 71:401–421.
- Kupferberg, S. J. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. *Ecology* 78:1736–1751.
- Lawler, S. P., D. Dritz, T. Strange, and M. Holyoak. 1999. Effects of introduced mosquitofish and bullfrogs on the threatened California red-legged frog. *Conservation Biology* 13:613–622.
- Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecological Applications* 18:1119–1139.
- MacKenzie, D. I., and L. L. Bailey. 2004. Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics* 9:300–318.
- MacKenzie, D. I., L. L. Bailey, and J. D. Nichols. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* 73:546–555.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy estimation and modeling*. Academic Press, Boston, Massachusetts, USA.
- Pearl, C. A., M. J. Adams, N. Leuthold, and R. B. Bury. 2005. Amphibian occurrence and aquatic invaders in a changing landscape: implications for wetland mitigation in the Willamette Valley, Oregon, USA. *Wetlands* 25:76–88.
- Pearl, C. A., M. J. Adams, R. B. Bury, and B. McCreary. 2004. Asymmetrical effects of introduced bullfrogs (*Rana catesbeiana*) on native ranid frogs in Oregon. *Copeia* 2004:11–20.
- Richter, K. O., and A. L. Azous. 1995. Amphibian occurrence and wetland characteristics in the Puget Sound basin. *Wetlands* 15:305–312.
- Schwalbe, C. R., and P. C. Rosen. 1988. Preliminary report on effects of bullfrogs on wetland herpetofaunas in southeastern Arizona. Pages 166–173 in R. C., Szaro, K. E., Severson, and D. R. Patton, editors *Technical coordinators. Management of amphibians, reptiles, and small mammals in North America*. US Department of Agriculture, Forest Service, GTR RM-166. Flagstaff, Arizona, USA.
- Semlitsch, R. D., and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17:1219–1228.

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