Conservation Biology

Contributed Paper

Factors Mediating Co-Occurrence of an Economically Valuable Introduced Fish and Its Native Frog Prey

ROSEMARY HARTMAN,* KAREN POPE,† AND SHARON LAWLER‡

*Graduate Group in Ecology, University of California, Davis, One Shields Avenue, Davis, CA 95616, U.S.A., email Rosehartman@gmail.com
†USDA Forest Service Pacific SW Research Station, Redwood Sciences Lab, 1700 Bayview Drive, Arcata, CA 95521-6013, U.S.A.
‡Department of Entomology, University of California, Davis, One Shields Avenue, Davis, CA 95616, U.S.A.

Abstract: *Habitat characteristics mediate predator–prey coexistence in many ecological systems but are seldom considered in species introductions. When economically important introduced predators are stocked despite known negative impacts on native species, understanding the role of refuges, landscape configurations, and community interactions can inform habitat management plans. We measured these factors in basins with introduced trout* (Salmonidae) *and the Cascades frog* (Rana cascadae) *to determine, which are responsible for observed patterns of co-occurrence of this economically important predator and its native prey. Large, vegetated shallows were strongly correlated to co-occurrence, and R. cascadae larvae occur in shallower water when fish are present, presumably to escape predation. The number of nearby breeding sites of R. cascadae was also correlated to co-occurrence, but only when the western toad* (Anaxyrus boreas) *was present. Because A. boreas larvae are unpalatable to fish and resemble R. cascadae, they may provide protection from trout via Batesian mimicry. Although rescue-effect dispersal from nearby populations may maintain co-occurrence, within-lake factors proved more important for predicting co-occurrence. Learning which factors allow co-occurrence between economically important introduced species and their native prey enables managers to make better-informed stocking decisions.*

Keywords: amphibians, conservation planning, facilitation, fisheries, freshwater, lake, predator indirect effects, refuges

Factores que Median la Co-Ocurrencia de un Pez Introducido con Valor Económico y su Presa, una Rana Nativa

Resumen: *Las características del hábitat median la co-existencia entre depredador y presa en muchos sistemas ecológicos pero rara vez se consideran en la introducción de especies. Cuando los depredadores introducidos con importancia económica son utilizados a pesar de tener un impacto negativo sobre las especies, entender el papel de los refugios, las configuraciones de paisaje y las interacciones de la comunidad puede informar a los planes de manejo de hábitat. Medimos estos factores en cuencas con truchas introducidas (Salmonidae) y la rana Rana cascadae para determinar cuáles son responsables de los patrones de co-ocurrencia de este depredador con importancia económica y su presa nativa. Bajíos grandes con vegetación estuvieron fuertemente correlacionados con la co-ocurrencia y las larvas de R. cascadae están presentes en aguas someras cuando los peces están presentes, presuntamente para escapar la depredación. El número de sitios de crianza de R. cascadae también estuvo correlacionado con la co-ocurrencia, pero sólo cuando el sapo Anaxyrus boreas estaba presente. Como las larvas de A. boreas no tienen buen sabor para los peces y se parecen a las de R. cascadae, puede que proporcionen protección de las truchas por medio de mimetismo batesiano. Mientras la dispersión efecto del rescate de las poblaciones cercanas puede mantener la co-ocurrencia, los factores internos del lago probaron ser más importantes para predecir la co-ocurrencia. Aprender cuáles factores permiten la co-ocurrencia entre las especies introducidas con importancia económica y sus presas nativas permite a los manejadores tomar decisiones de uso mejor informadas.*

Palabras Clave: Agua dulce, anfibios, efectos indirectos de depredación, facilitación, lago, pesquerías, planificación de la conservación, refugio

Paper submitted May 3, 2013; revised manuscript accepted August 18, 2013.

Conservation Biology, Volume 28, No. 3, 763–772

DOI: 10.1111/cobi.12218

Introduction

Invasive species are a leading threat facing world biodiversity (Mack et al. 2000; Blackburn et al. 2010), but many introduced species are intentionally stocked and maintained despite negative effects on native species. These cultivated introduced species pose a difficult problem because, unlike purely detrimental species, they have economic and cultural value. Examples include agriculturally important plants and animals, biocontrol agents, ornamentals, pets, and game fish. For these organisms, plans for eradication and even containment are contentious.

The emerging field of reconciliation ecology advocates for a shift in management from preserving only pristine communities to fostering native species in anthropogenically modified communities (Rosenzweig 2003). Much of the literature on species invasions focuses on removal and suppression (Blackburn et al. 2010), but reconciliation ecology suggests managed coexistence as a possible solution. For example, refuges buffer the effect of invasive species in many systems (Milchunas & Noy-Meir 2002; Westhoff et al. 2013); however, this concept is seldom used to plan intentional introductions.

Using the case study of the Cascades frog (*Rana cascadae*) and introduced trout (Salmonidae), we analyzed how a native species of conservation concern coexists with a culturally and economically important introduced predator. Fish are one of the most commonly stocked predatory taxa worldwide (Cambray 2003), and salmonids are culturally and economically important in the lakes and streams of every continent except Antarctica (Crawford & Muir 2008). Trout and char (*Oncorhynchus* spp., *Salmo* spp., and *Salvelinus* spp.) have had well-documented negative effects on native fishes, invertebrates, and amphibians wherever they have been introduced (Knapp et al. 2001; Crawford & Muir 2008; Pope et al. 2009). The effects on amphibians occurring in historically fishless aquatic systems have been especially severe (e.g., Pilliod & Peterson 2001; Vredenburg 2004; Hartel et al. 2007). For example, three of California's native ranid frogs (*R. cascadae*, *R. muscosa*, and *R. sierrae*) occur in historically fishless mountain lakes and are negatively impacted by fish introductions (Knapp & Matthews 2000; Vredenburg 2004; Welsh et al. 2006). These findings led to a successful lawsuit in which the California Superior Court ruled that the California Department of Fish and Wildlife (CDFW) must consider the effects of fish stocking on sensitive aquatic species when making stocking decisions (Pacific Rivers Council & Center for Biological Diversity v. CDFW. 2007. Case number 06CS01451, California Superior Court). However, recreational fisheries are an important economic and cultural part of the human community in these areas (Knapp et al. 2001). Identifying key factors that allow for co-occurrence of amphibians and non-native fish provides insight into ways to reconcile the often-conflicting goals of managing for both native amphibians and recreational fisheries.

We sought to describe how refuge habitat, landscape configurations, and multispecies interactions influence co-occurrence of a native species and an economically important predator; compared prey refuge use when predators are present versus absent; and developed predictions of where trout may co-occur with native prey so as to inform recommendations on whether to stock trout in certain areas.

Local habitat characteristics, landscape connectivity, and community assemblages influence outcomes of invasive and native species interactions, but teasing apart the importance of the influences is key for promoting coexistence. Within-lake features such as extended shallows and aquatic vegetation in which frog larvae can avoid predation may allow *R. cascadae* to co-occur with fish (Porej & Hetherington 2005; Van Buskirk 2005; Hartel et al. 2007). Alternatively, the larger landscape may more strongly affect predator–prey dynamics on the local scale. Predator-free habitat patches may have higher prey species density than invaded patches and thus lead to rescue-effect dispersal from the predator-free patches to invaded patches. This increases the possibility of co-occurrence in invaded patches (Brown & Kodric-Brown 1977) and may allow long-term coexistence on a regional scale. There is also the opportunity for diverse indirect effects of competitors, other predators, and prey species on the interaction between native prey and introduced predators (White et al. 2006). Legislation requires that species of conservation concern such as *R. cascadae* be protected, but traditional management may overlook the potential to take advantage of mutualistic interactions by species not protected by law (Halpern et al. 2007). Assessing the distribution of species that potentially provide defenses or resources for protected taxa may lead to greater success in conservation and restoration projects.

Refuge habitat is most effective if the prey uses the refuge when predators are present, so we also tested whether the native prey occupied refuge habitats more when their non-native predator was present. Because these species did not coexist in evolutionary time, the prey may not have evolved anti-predator behaviors (Sih et al. 2010). However, if *R. cascadae* do actively use refuges in response to trout, behavior may act synergistically with refuges to enhance survival.

To investigate factors that allow these species to co-occur, we used predictive modeling to assess the importance of the local and landscape-scale factors described earlier for predicting co-occurrence. Although long-term monitoring will be necessary to determine if these populations can coexist in the long term, patterns of co-occurrence provide a baseline for future studies. This type of predictive modeling may also be used to guide management not only of salmonids around the globe (Crawford & Muir 2008), but also of a diverse array of

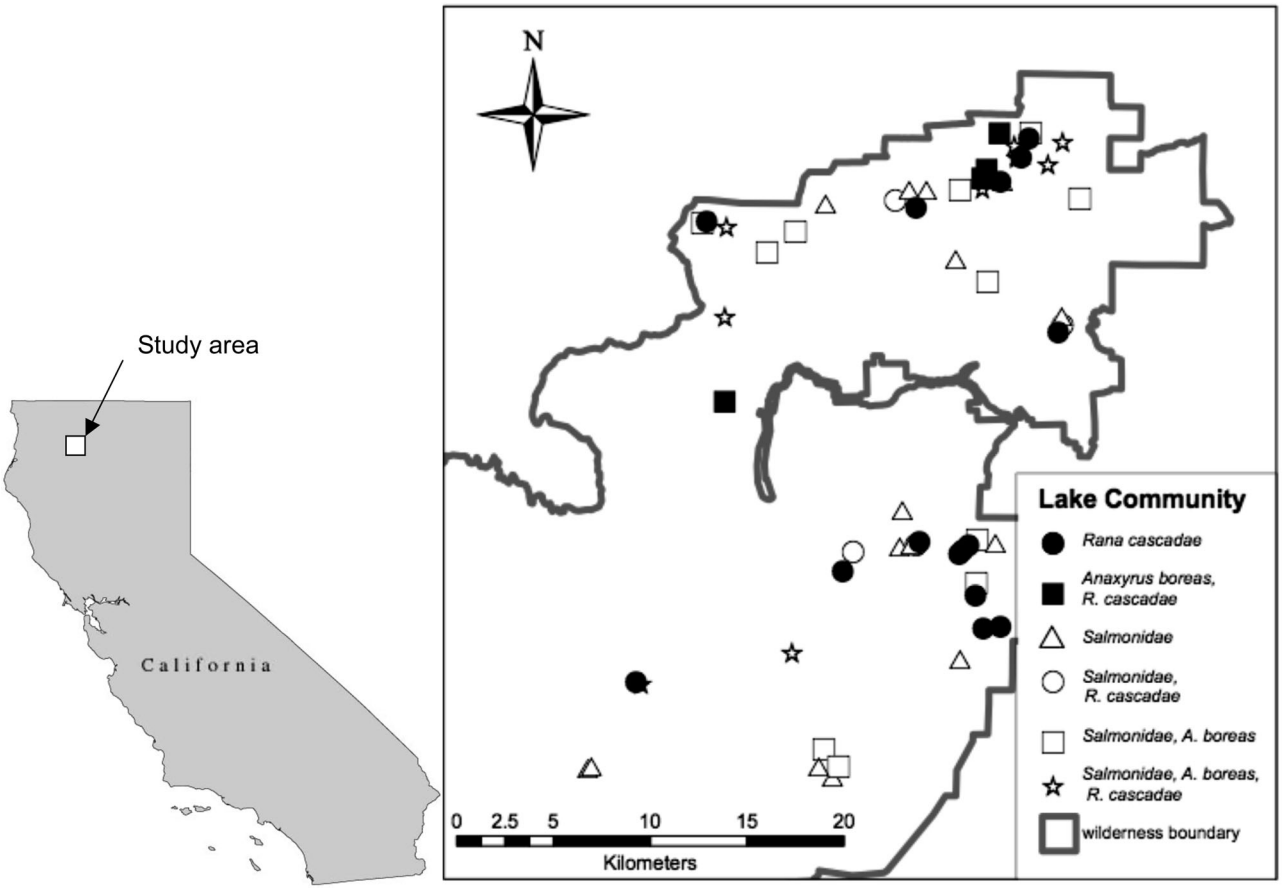

Figure 1. Map of the study area in northern California (U.S.A.). Symbols indicate aquatic community.

other non-native fisheries (Cambray 2003), agricultural systems (Milchunas & Noy-Meir 2002; Callaway et al. 2005), and systems where economically important introduced consumers dominate the community (Schlaepfer et al. 2011). Even without modeling, consideration of refuge habitat and management for coexistence between native and introduced species may reduce conflict between conservation and economic goals in a socio-ecological system.

Methods

Study Site

The Trinity Alps Wilderness is a federally designated wilderness area in the Klamath Mountains of northern California (U.S.A.). It is managed for wilderness recreation and cattle grazing, but logging, road building, and mechanized vehicles are prohibited. It contains hundreds of lakes and ponds, most between 1550 and 2300 m in elevation. Glaciation of these mountains restricted fish colonization above 1500 m (Welsh et al. 2006). Beginning in the 1920s, most lakes greater than 1 m in depth were stocked with brown trout, brook trout, and rainbow trout by CDFW (Crawford & Muir 2008). There are now self-sustaining populations of brook trout present in most lakes greater than 3 m in depth. A subset of these lakes is still stocked yearly with rainbow trout by CDFW (B. Aguilar, personal communication). Because the majority of fish in the system are brook trout and rainbow trout and previous studies have found no difference between these trout species in their effect on amphibians (Vredenburg 2004; Welsh et al. 2006), we combined stocked fish (hereafter "trout") for analysis.

Field Sampling

To test whether refuge habitat facilitates co-occurrence between amphibians and introduced trout, we surveyed 62 water bodies (permanent lakes and ponds, hereafter lakes) in the Trinity Alps during the summers of 2011 and 2012 (Fig. 1). Sampling was stratified to include similar representation of three lake types. Eighteen lakes contained both trout and breeding *R. cascadae*, 24 contained trout without breeding *R. cascadae*, and 20 contained breeding *R. cascadae* without trout.

Previous visual encounter surveys of *R. cascadae* found very high detection probabilities ($p > 0.9$) (Piovia-Scott et al. 2011), so we used these methods to assess amphibian presence at each lake (described in Crump & Scott

1994). *R. cascadae* is a large (5–10 cm at adulthood), long-lived (10–12 years) frog that occurs in a wide variety of lakes, ponds, and meadows and requires shallows for breeding and open canopies for basking (Briggs 1987; Welsh et al. 2006). Larvae metamorphose within one summer, but all life stages remain close to water. We also surveyed western toad (*Anaxyrus boreas*), Pacific tree frog (*Pseudacris regilla*), Pacific giant salamander (*Dicamptodon tenebrosus)*, and rough-skinned newt *(Taricha granulosa)*.

At 24 evenly spaced transects around each lake, we measured shallow area, vegetation, littoral zone slope, and percent silt, all characteristics we hypothesized are associated with amphibian refuges. We measured distance from shore to 10 cm, 50 cm, and 100 cm depth and regressed these distances with ordinary least squares to calculate a value for average littoral zone slope. We measured distance from shore to the end of emergent aquatic vegetation and multiplied the average value by the perimeter of the lake to calculate lake area covered by aquatic vegetation. At each point along the transect, we recorded substrate of the lakebed to calculate the percentage of the substrate dominated by silt. While surveying, we recorded the distance from shore and depth of all amphibian larvae. We used CDFW's recent trout stocking records and gill net surveys from 1999 to 2012 (unpublished data) and visual encounter surveys to determine trout presence or absence at each lake. The CDFW data came from stocking assessments consisting of 4-hour variable-mesh gill net sets in the deepest part of the lake being surveyed and a visual encounter survey for amphibians.

Geographic Analyses

To measure distance to nearby *R. cascadae* breeding habitat, we used data from surveys of trout and amphibians in every water body in the Trinity Alps Wilderness conducted by USDA Forest Service's Pacific Southwest Research Station between 1999 and 2002 (Welsh et al. 2006). This data set was updated with data from CDFW's fish stocking surveys from 2002 to 2012 (unpublished data) and data from Piovia-Scott et al.'s (2011) surveys of 112 known *R. cascadae* breeding sites in 2008. Piovia-Scott et al. (2011) found *R. cascadae* at 79% of sites where they were seen in 1999–2002, so the data points in our combined data set reflected actual or historical *R. cascadae* presence. Lakes that shared a watershed were grouped into basins separated by ridges high enough to present a barrier to frog movement (Pilliod & Peterson 2001). For each of our study lakes, we computed number of other water bodies and number of *R. cascadae* breeding sites (source populations) within the same basin. To generate landscape cover values, we used CalvegTiles_Ecoregions07_4, a LANDSAT data set that classifies major vegetation types of California (USDA Forest Service Remote Sensing Lab 2010), to calculate the amount of herbaceous vegetation cover (meadows), woody vegetation, and nonvegetated area within each basin. All geographic data analyses were performed on ArcGIS 10 (ESRI, Redlands, CA, USA).

Statistical Analyses

We built a model that predicted lakes in which *R. cascadae* were most likely to coexist with trout by building a series of descriptive generalized linear models with the data on within-lake habitat variables and basin characteristics for lakes containing trout ($n = 42$). Candidate variables were selected a priori based on previous amphibian models and field observations: area of emergent aquatic vegetation, littoral zone slope, percentage of silt, presence of *A. boreas* larvae, proportional cover of herbaceous vegetation in the basin, number of lakes in the basin, and number of frog populations in the basin (Table 1). Area of emergent vegetation was log transformed and proportional data were transformed to the arcsine square root to meet assumptions of normality. We left *P. regilla* out of model selection because they are also palatable to trout and so are likely to respond to the same habitat variables as *R. cascadae*. *Taricha granulosa* and *Dicampodon tenebrosus* were not present in enough lakes to affect model fit. We ranked all possible models containing candidate variables with Akaike's information criterion corrected for small sample sizes (AICc) to find which model maximized the likelihood of the model given the data while penalizing more complex models (Anderson 2008).

To determine which variables were most important when developing a predictive model, we also calculated AICc weights for each variable. AICc weights are calculated by summing the delta AICc values for all models including a given factor and scaling them to be between 0 and 1 (Anderson 2008).

All 13 potential combinations of the four most important variables were ranked via AICc to determine the final predictive model. We limited these models to only four terms to avoid overfitting (Anderson 2008). We averaged parameter estimates across all models that were within delta AICc < 6 of the best model (Richards 2008).

To assess goodness of fit and evaluate model utility, we performed leave-one-out cross validation (similar to Knapp et al. 2003). This gives a within-sample error rate of the model. We compared this to the area under the receiver-operating characteristic curve (AUC), which is commonly used to assess model fit in presence–absence models. Values closer to 1 indicate better model fit, and values closer to 0.5 are equivalent to the null model (Jiménez-Valverde 2012).

We determined if refuge use by larvae of *R. cascadae* and *A. boreas* varied in lakes with and without trout ($n = 62$) by building a generalized linear mixed model

Table 1. Terms used in construction of the descriptive model of likelihood of co-occurrence between *R. cascadae* and introduced trout.

Term	*Spatial extent*	*Co-occurrence lakes mean (SE)*	*Trout lakes mean (SE)*	*Overall mean (SE)*	*Relative importance*[a]	*Explanation*
Bank slope	local	0.14 (0.13)	0.30 (0.083)	0.23 (0.14)	1	average slope of lake littoral zone
A. boreas	local	13/18	9/24	21/42	0.71	presence of *A. boreas* larvae in lake
A. boreas by source populations	local and landscape	NA	NA	NA	0.67	interaction between presence of *A. boreas* and number of *R. cascadae* breeding sites
Vegetated area	local	2.79 (0.43)	1.96 (1.04)	2.32 (0.92)	0.34	log-transformed area of emergent aquatic vegetation in lake
Herbaceous cover	landscape	0.20 (0.14)	0.15 (0.14)	0.05 (0.05)	0.31	proportion of basin covered by herbaceous vegetation transformed to arcsine square root
Lakes	landscape	3.61 (2.64)	2.92 (3.40)	3.21 (3.08)	0.16	number of lakes in surrounding basin
Silt	local	1.17 (0.29)	0.91 (0.34)	0.69 (0.25)	0.15	proportion of percent silt in lake substrate transformed to arcsine square root
Source populations	landscape	1.33 (1.37)	1.42 (1.91)	1.38 (1.68)	0.02	number of *R. cascadae* breeding sites in surrounding basin

[a]*All models including combinations of these terms were ranked via Akaike's information criterion corrected for small sample size and the relative importance of each term was calculated for the top 20 models.*

Table 2. Full-model averaged coefficients* with shrinkage for terms in the final averaged model of *R. cascadae* and trout co-occurrence, the coefficient standard errors, odds ratios (ORs), and confidence intervals for the ORs.

				Confidence interval	
Model-averaged coefficients	*Relative importance*	*Estimate (SE)*	*OR*	*2.5%*	*97.5%*
Intercept		0.997 (3.55)	2.710	0.00257	2864.4
Bank slope	1	−19.706 (7.15)	2×10^{-9}	7×10^{-16}	0.0099
Vegetated area (m^2)	0.5	0.911 (1.312)	2.49	0.37833	103.34
Source populations: *A. boreas* absent	0.9	−0.988 (1.025)	0.372	0.03785	2.9388
Source populations: *A. boreas* present	0.9	1.055 (0.638)	2.87	0.8462	12.33
A. boreas (main effect)	0.29	0.163 (0.766)	1.18	0.04154	73.479

[a]*The final model was constructed by averaging the top six models from the candidate model rankings, which together made up 96% of the AICc weight.*

with depth of larvae as the response variable, trout presence or absence as the predictor, and lake as a random effect. We calculated *p* values with Markov-chain Monte Carlo simulation (Anderson 2008). All statistical analyses were performed with R (packages bbmle, pROC, MuMIn, and languageR) (R project for statistical computing, 2012).

Results

Descriptive and Predictive Models

Local variables explained much of the co-occurrence between *R. cascadae* and trout (Table 1). Probability of co-occurrence was improved by low littoral slope, the presence of *A. boreas*, large extents of vegetation within the lake, and number of *R. cascadae* breeding sites within the same basin when *A. boreas* were present. Other landscape variables were not included in the best-supported models.

The averaged model included a very strong negative effect of littoral zone slope (odds ratio [OR] = $2.77 \times 10 - 1$), such that a 0.1 increase in slope decreased the odds of co-occurrence by a factor of 0.14. There was a weaker positive effect of vegetated area (OR = 2.49), a large positive effect of number of *R. cascadae* breeding sites within the same basin when *A. boreas* were present (OR = 2.87), a weaker negative effect of number of *R. cascadae* breeding sites within the same basin when *A. boreas* were absent (OR = 0.37), and a slight positive main effect of *A. boreas* presence (OR = 1.18) (Table 2 & Fig. 1). Six of the 13 potential models with the four most important variables were within six AICc units of each other and accounted for 97% of the AICc weights. The final model was constructed by averaging these six models and was effective at explaining presence of *R. cascadae* in lakes that contained trout with an AUC score of 0.9444 and an error rate of 26.2% from within-sample cross validation.

Habitat Use

R. cascadae tadpoles were found in water that was 7.6 cm (SE = 2.8) shallower in lakes with trout than in lakes that did not contain trout ($p = 0.006$). This shift in

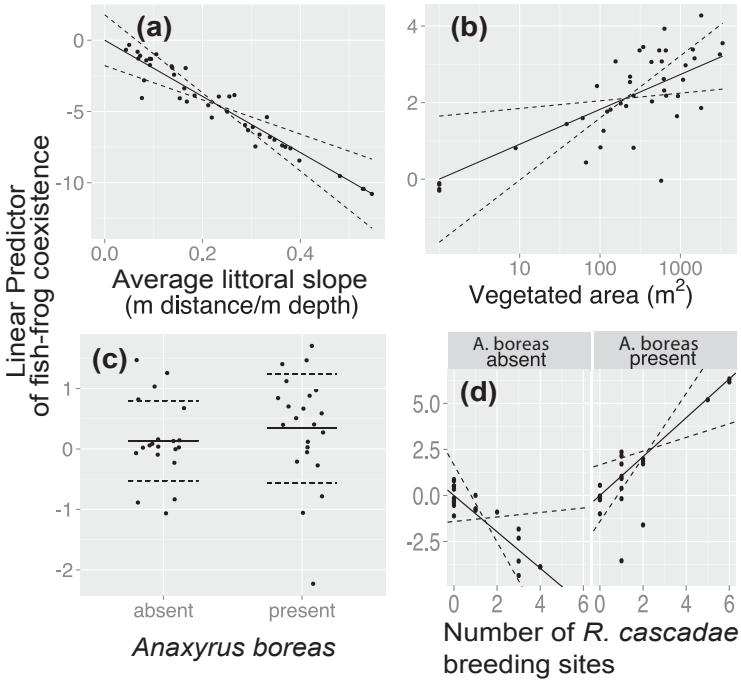

Figure 2. Effect of (a) littoral slope, (b) vegetated area, (c) presence of A. boreas, and (d) number of R. cascadae breeding sites in the basin on probability of co-occurrence (1 SE) between R. cascadae and introduced trout when all other terms are controlled.

average depth was due to fewer tadpoles being found in the deeper end of their range rather than an increase in tadpoles observed in the shallower end of the range (Fig. 3). When averaged across both types of lakes *R. cascadae* larvae were found in water that was 9.1 cm (SE = 4.1) shallower than water in which *A. boreas* larvae ($p = 0.001$) were found. *A. boreas* were not observed in statistically different depths when fish were present ($p = 0.24$).

Discussion

This study demonstrates that predator–prey theory can be used to successfully identify important correlates of co-occurrence between stocked predators and native prey. Refuge habitats were the most important correlate, followed by presence of a similar, but unpalatable species. Finding that the native prey species occurred in refuge habitats more often when predators were present suggests that prey may be able to respond behaviorally even when they do not share recent evolutionary history with their predator. Our model provides specific, measurable traits of lakes that can be used to inform trout stocking decisions when combined with active monitoring of amphibian populations.

Refuge habitats within the focal lake improved the probability of co-occurrence. Several types of refuges mediate the effect of invaders in other systems and increase prey survival (Westhoff et al. 2013) and native species biodiversity (Milchunas & Noy-Meir 2002). Shallow vegetated areas are important refuges for amphibian larvae (Porej & Hetherington 2005), and *R. cascadae* were found in shallows more often when trout were present (Fig. 2). Refuge habitats are also important for coexistence of trout and aquatic macroinvertebrates, an important food source for adult frogs and many other members of the terrestrial community (Pope & Hannelly 2013).

Welsh et al. (2006) developed a similar model for all water bodies (with and without trout) and found that absence of trout, a high percentage of silt, and large lake perimeters were predictive of *R. cascadae* larval presence. Because trout are more likely to occur in larger lakes, any silty lake in the area that can support trout may be able to support *R. cascadae* when trout are removed. A larger lake with extensive vegetated shallows is more likely to support both frogs and trout, whereas lakes with fewer vegetated shallows would likely only support one or the other and could be targeted for trout removal to restore frog populations.

There are multiple examples of indirect interactions changing the relationship between predators and prey in invasion ecology (reviewed in White et al. 2006). The presence of *A. boreas* improved the likelihood of *R. cascadae* and trout co-occurrence, both on its own and as an interaction with source populations. This may be because *A. boreas* and *R. cascadae* have similar habitat requirements to successfully co-occur with trout. Both species lay eggs in shallow, vegetated water (Briggs 1987; Olson 1988); however, their larvae habitats are very different. *A. boreas* larvae are unpalatable to trout, so they are not restricted to the shallow areas that *R. cascadae* uses (Welsh et al. 2006). We observed *A. boreas* occupying significantly deeper water than *R. cascadae* (Fig. 2), and there was no association between habitat used by

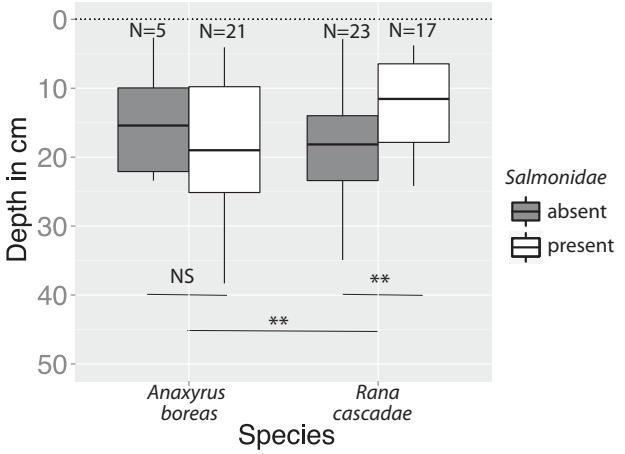

*Figure 3. Average depth (1 SE) of A. boreas and R. cascadae larvae observed in lakes with and without trout (Salmonidae). Depth values were averaged within lakes before being compared across lakes (**$p < 0.01$).*

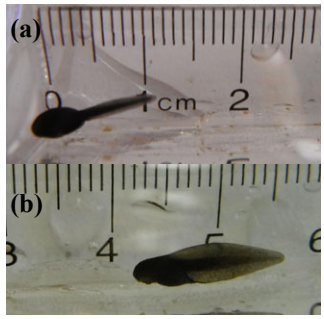

Figure 4. (a) A. boreas larvae and (b) R. cascadae larvae at 7 days of age.

A. boreas and trout presence. Therefore, there was little support for the hypothesis that *A. boreas* and *R. cascadae* respond similarly to habitats in lakes containing fish.

The interaction may also be caused by the two amphibians responding to similar disease dynamics. The fungus *Batrachochytrium dendrobatidis* (Bd) is a pathogenic chytrid that causes the amphibian disease chytridiomycosis. This disease occurs throughout the Klamath Mountains (Piovia-Scott et al. 2011) and has been implicated in declines of both *R. cascadae* and *A. boreas* (Muths et al. 2003; Fellers et al. 2008). The presence of *A. boreas* may indicate that a given lake is clear of the more virulent strains of Bd. However, in the same study region as ours, Piovia-Scott et al. (2011) did not find a correlation between the presence of *A. boreas* and prevalence of Bd. Although assessment of this disease was beyond the scope of this study, disease and predation may interact to influence *R. cascadae* presence in lakes that contain trout.

An alternate hypothesis is that the presence of *A. boreas* indirectly reduces predation pressure on *R. cascadae*. This is similar to the associational defenses of unpalatable plants, which increase native plant diversity in systems where non-native herbivores are stocked for agricultural purposes (Callaway et al. 2005), and it has been suggested that planting unpalatable species may promote co-occurrence between cattle and native plants (King & Stanton 2008). *R. cascadae* and *A. boreas* larvae are visually very similar (Fig. 4), especially at early stages of development when they are most vulnerable to trout predation. Encounters with unpalatable *A. boreas* larvae may discourage trout from attempting to consume any similar looking amphibian larvae, through a mechanism similar to Batesian mimicry. In a similar situation, Nelson et al. (2010) demonstrated that unpalatable *Bufo marinus* larvae protected a palatable amphibian from trout predation in the lab. Because *A. boreas* are explosive breeders that hatch at the same time as *R. cascadae* (Olson 1988), their larvae are usually much more abundant than larvae of *R. cascadae*. They also occupy deeper water than *R. cascadae* (Fig. 2), so trout will be more likely to encounter *A. boreas* larvae than *R. cascadae* larvae. Models of Batesian mimicry indicate that higher encounter rates with unpalatable prey greatly increase value of mimicry for the palatable mimic (Lindström et al. 1997).

In our study, the presence of predators altered the roles of local and landscape criteria in predicting distribution of prey species. Although population distribution of highly mobile species, such as birds or butterflies, is affected mainly by landscape factors (Hanski & Thomas 1994; Betts et al. 2007), we found local factors more important than landscape factors when predicting where *R. cascadae* would coexist with trout. In contrast, several other studies of amphibians show that landscape scale factors best predict presence and absence (Price et al. 2005; Scherer et al. 2012). More often, both local and landscape factors influence distributions of metapopulations (Pilliod & Peterson 2001; Van Buskirk 2005; Welsh et al. 2006). However, most of the above-mentioned studies include presence of predators in their model but do not compare the effects of other factors when predators are present versus when they are absent. The effect of trout in this system is large, as has been shown by previous work on the *R. cascadae* (Welsh et al. 2006; Pope 2008), and because trout are restricted to the aquatic environment they may have higher local influence than landscape influence.

The landscape variable that had support in the final model was *R. cascadae* breeding sites within a basin. Proximity to nearby breeding sites is important for other montane amphibians (Pilliod & Peterson 2001; Knapp et al. 2003). Nearby populations provide a rescue effect whereby frogs occasionally disperse to lakes with trout and maintain apparent fish–frog coexistence (Brown & Kodric-Brown 1977).

R. cascadae larvae were found in shallows more often when trout were present (Fig. 2), which may indicate successful use of this refuge habitat. Two mechanisms may drive this relationship: either larvae avoided deep water when trout were present or larvae that entered deeper water were eaten before they were observed. Behavioral studies investigating which mechanism is in play may be important to deciding whether trout and native species can coexist indefinitely or whether frog populations in lakes where they co-occur with trout are more likely to be extirpated. Some studies show amphibians and other taxa develop antipredator responses to introduced species (Capps et al. 2009; D'Amore et al. 2009), so there may be the capacity for *R. cascadae* to develop appropriate defenses.

Refuge use often incurs fitness consequences (as reviewed in Orrock et al. 2013), and these consequences may mean co-occurring populations will not persist in the long term. *R. cascadae* reduced their average depth in the presence of fish, reducing the amount of habitat and associated resources by up to one-third, which may affect larval growth rate and survival. It may also make them more vulnerable to terrestrial predators. The extent to which refuge use affects *R. cascadae's* fitness may be key in determining whether these lakes can support long-term predator–prey coexistence.

The important factors in this model may be used to prioritize stocking decisions. The low importance of landscape variables means stocking decisions are more critical than landscape use practices. However, if enough nearby patches are free from introduced predators, then dispersers may be able to support a population in a stocked lake, especially when unpalatable species are present. In some systems, it may even be possible to increase the amount of refuges available to allow native species to coexist with non-natives (Westhoff et al. 2013).

The strong positive relationship between two prey species highlights the importance of considering community interactions when determining management priorities. Presence of the unpalatable *A. boreas* was an indicator of increased likelihood that *R. cascadae* would coexist with introduced trout, regardless of the mechanism behind the relationship. If the unpalatable species provides protection through mimicry, it may mean that both species are of conservation concern, though the unpalatable species is not currently undergoing population decline. If a shared pathogen is the cause of the relationship, the situation warrants further research because disease is more difficult to control than stocking decisions. Even in a patch with ideal conditions for co-occurrence, disease may act synergistically with predation to extirpate a population (Fellers et al. 2008).

Using the methods described here, models of refuges and unpalatable species mediating coexistence of economically important introduced species and native species may be developed for other systems. Even when a complex model is impractical, the important factors predicting predator–prey coexistence can be applied for conservation or restoration. Introduced species may be stocked without threatening native populations if these can persist due to large extents of refuges, unpalatable species, or immigration. In systems where stocking decisions have already been made, refuges may be constructed or unpalatable species may be introduced. For example, cattle and other agricultural animals may have negative effects on native plant species diversity. To counter this, cattle can be preferentially pastured in areas with thorny nurse shrubs to increase grass abundance (Callaway et al. 2005). In areas that are already heavily grazed, unpalatable species such as aloe or thorn bushes may be introduced to provide protection for native species (King & Stanton 2008). Ungrazed areas can be interspersed with grazed areas across the landscape to provide rescue-effect dispersal (Milchunas & Noy-Meir 2002).

Managing for coexistence rather than elimination of introduced species may be useful, but close monitoring of native species is equally important. Our model describes characteristics of lakes most likely to contain both trout and *R. cascadae*, but it does not support blanket stocking of any one type of lake. The AUC score of 0.94 indicated a high degree of model fit; however, the relatively high (26%) error rate means it may not be accurate in other areas. The model is designed to be one tool among many when choosing between lakes for trout stocking or removal, and it should only be relied on when accompanied by continued amphibian monitoring. Furthermore, it may be too soon to tell whether current breeding populations have long-term viability; slow declines may indicate trout are causing an extinction debt that could cause increased susceptibility to other threats such as disease, pollution, and climate change (Blaustein & Kiesecker 2002).

It is infeasible to assume that economically and culturally important non-natives will always be eliminated from protected areas even if detrimental effects to native species are documented. Introduced trout continue to be stocked in lakes and streams worldwide despite dramatic negative effects on native fauna (Crawford & Muir 2008). Given the persistence of introduced trout in natural reserves, our study improves understanding of conditions that promote persistence of sensitive native amphibians within a modified community structure. Within-lake refuge habitats and presence of a prey species that is unpalatable to trout greatly influenced the ability of *R. cascadae* to coexist with trout. Landscape connectivity was also important but only when the unpalatable, *A. boreas*, was present. We are unsure of the mechanism underlying this relationship, but our findings highlight the importance of facultative interactions in predator–prey dynamics. In any system where introduced species have important economic and recreational functions, it may be wise to study ways to encourage co-occurrence

with native species, in addition to providing habitat for the native taxa alone.

Acknowledgments

We thank R. Smith, R. Gutstein, and many other field assistants, H. Welsh and the USFS for use of their data, and B. Aguilar of CDFW for field equipment and trout survey data. We thank two anonymous reviewers whose comments significantly improved the manuscript. This study was funded by grants from the Amphibian and Reptile Conservancy, the California Fly Fishers Unlimited, Marin Rod and Gun Club, and the UC Davis Jastro Research Fellowship.

Literature Cited

Anderson, D. R. 2008. Model-based inference in the life sciences: a primer on evidence. Springer, New York.

Betts, M. G., G. J. Forbes, and A. W. Diamond. 2007. Thresholds in songbird occurrence in relation to landscape structure. Conservation Biology **21:**1046–1058.

Blackburn, T. M., N. Pettorelli, T. Katzner, M. E. Gompper, K. Mock, T. W. J. Garner, R. Altwegg, S. Redpath, and I. J. Gordon. 2010. Dying for conservation: eradicating invasive alien species in the face of opposition. Animal Conservation **13**:227–228.

Blaustein, A. R., and J. M. Kiesecker. 2002. Complexity in conservation: lessons from the global decline of amphibian populations. Ecology Letters **5:**597–608.

Briggs, J. L. 1987. Breeding biology of the Cascade frog, *Rana cascadae,* with comparisons to *R. aurora* and *R. pretiosa*. Copeia **1987:**241–245.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology **58:**445–449.

Callaway, R. M., D. Kikodze, M. Chiboshvili, and L. Khetsuriani. 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. Ecology **86:**1856–1862.

Cambray, J. A. 2003. Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. Hydrobiologia **500:** 217–230.

Capps, K. A., C. B. Turner, et al. 2009. Behavioral responses of the endemic shrimp *Halocaridina rubra* to an introduced fish, *Gambusia affinis* and implications for the trophic structure of Hawaiian anchialine ponds. Pacific Science **63:**27–37.

Crawford, S., and A. Muir. 2008. Global introductions of salmon and trout in the genus *Oncorhynchus:* 1870–2008. Reviews in Fish Biology and Fisheries **18:**313–344.

Crump, M. L., and N. J. Scott. 1994. Visual encounter surveys. Pages 84–92 in W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. A. C. Hayek, and M. S. Foster, editors. Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution, Washington, DC.

D'Amore, A., E. Kirby, and M. McNicholas. 2009. Invasive species shifts ontogenetic resource partitioning and microhabitat use of a threatened native amphibian. Aquatic Conservation: Marine Freshwater Ecosystems **19:**534–541.

Fellers, G. M., K. L. Pope, J. E. Stead, M. S. Koo, and H. H. Welsh Jr. 2008. Turning population trend monitoring into active conservation: Can we save the Cascades frog in the Lassen Region of California? Herpetological Conservation and Biology **3:**28–39.

Halpern, B. S., B. R. Silliman, J. D. Olden, J. P. Bruno, and M. D. Bertness. 2007. Incorporating positive interactions in aquatic restoration and conservation. Frontiers in Ecology and the Environment **5:** 153–160.

Hanski, I., and C. D. Thomas. 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. Biological Conservation **68:**167–180.

Hartel, T., S. Nemes, D. Cogalniceanu, K. O. llerer, O. Schweiger, C.-I. Moga, and L. Demeter. 2007. The effect of fish and aquatic habitat complexity on amphibians. Hydrobiologia **583:**173–182.

Jiménez-Valverde, A. 2012. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. Global Ecology and Biogeography **21:**498–507.

King, E. G., and M. L. Stanton. 2008. Facilitative effects of aloe shrubs on grass establishment, growth, and reproduction in degraded Kenyan rangelands: implications for restoration. Restoration Ecology **16:**464–474.

Knapp, R. A., and K. R. Matthews. 2000. Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. Conservation Biology **14:**428–438.

Knapp, R. A., P. S. Corn, and D. E. Schindler. 2001. The introduction of nonnative fish into wilderness lakes: good intentions, conflicting mandates, and unintended consequences. Ecosystems **4:** 275–278.

Knapp, R. A., K. R. Matthews, H. K. Preisler, and R. Jellison. 2003. Developing probabilistic models to predict amphibian site occupancy in a patchy landscape. Ecological Applications **13:**1069–1082.

Lindström, L., R. V. Alatalo, and J. Mappes. 1997. Imperfect Batesian mimicry: the effects of the frequency and the distastefulness of the model. Proceedings of the Royal Society of London **264:**149–153.

Mack, R. N., D. Simberloff, W. Mark Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications **10:**689–710.

Milchunas, D. G., and I. Noy-Meir. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. Oikos **99:**113–130.

Muths, E., P. Stephen Corn, A. P. Pessier, and D. Earl Green. 2003. Evidence for disease-related amphibian decline in Colorado. Biological Conservation **110:**357–365.

Nelson, D. W. M., M. R. Crossland, and R. Shine. 2010. Indirect ecological impacts of an invasive toad on predator-prey interactions among native species. Biological Invasions **12:**3363–3369.

Olson, D. H. 1988. The ecological and behavioral dynamics of breeding in three sympatric anuran amphibians. Doctoral dissertation in zoology, Oregon State University, Eugene, OR.

Orrock, J. L., E. L. Preisser, J. H. Grabowski, and G. C. Trussell. 2013. The cost of safety: refuges increase the impact of predation risk in aquatic systems. Ecology **94:**573–579.

Pilliod, D. S., and C. R. Peterson. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. Ecosystems **4:**322–333.

Piovia-Scott, J., K. L. Pope, S. P. Lawler, E. M. Cole, and J. E. Foley. 2011. Factors related to the distribution and prevalence of the fungal pathogen *Batrachochytrium dendrobatidis* in *Rana cascadae* and other amphibians in the Klamath Mountains. Biological Conservation **144:**2913–2921.

Pope, K. L. 2008. Assessing changes in amphibian population dynamics following experimental manipulations of introduced fish. Conservation Biology **22:**1572–1581.

Pope, K., and E. Hannelly. 2013. Response of benthic macroinvertebrates to whole-lake, non-native fish treatments in mid-elevation lakes of the Trinity Alps, California. Hydrobiologia **714**:201–215.

Pope, K. L., J. Piovia-Scott, and S. P. Lawler. 2009. Changes in aquatic insect emergence in response to whole-lake experimental manipulations of introduced trout. Freshwater Biology **54:**982–993.

Porej, D., and T. E. Hetherington. 2005. Designing wetlands for amphibians: the importance of predatory fish and shallow littoral zones in structuring of amphibian communities. Wetlands Ecology and Management **13:**445–455.

Price, S. J., D. R. Marks, R. W. Howe, J. M. Hanowski, and G. J. Niemi. 2005. The importance of spatial scale for conservation and assessment of Anuran populations in coastal wetlands of the Western Great Lakes, USA. Landscape Ecology **20:**441–454.

Richards, S. A. 2008. Dealing with overdispersed count data in applied ecology. Journal of Applied Ecology **45:**218–227.

Rosenzweig, M. L. 2003. Reconciliation ecology and the future of species diversity. Oryx **37:**194–206.

Scherer, R., E. Muths, and B. Noon. 2012. The importance of local and landscape-scale processes to the occupancy of wetlands by pond-breeding amphibians. Population Ecology **54:**487–498.

Schlaepfer, M. A., D. F. Sax, and J. D. Olden. 2011. The potential conservation value of non-native species. Conservation Biology **25:**428–437.

Sih, A., et al. 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos **119:**610–621.

USDA Forest Service Remote Sensing Lab. 2010. CalvegTiles_Ecoregions07_4, Pacific Southwest Region Research Station, McClellen, CA.

Van Buskirk, J. 2005. Local and landscape influence on amphibian distribution and abundance. Ecology **86:**1936–1947.

Vredenburg, V. T. 2004. Reversing introduced species effects: experimental removal of introduced fish leads to rapid recovery of a declining frog. Proceedings of the National Academy of Sciences of the United States of America **101:**7646–7650.

Welsh, H. H., K. L. Pope, and D. Boiano. 2006. Sub-alpine amphibian distributions related to species palatability to non-native salmonids in Klamath mountains of northern California. Diversity and Distributions **12:**298–309.

Westhoff, J. T., A. V. Watts, and H. T. Mattingly. 2013. Efficacy of artificial refuge to enhance survival of young Barrens topminnows exposed to western mosquitofish. Aquatic Conservation: Marine and Freshwater Ecosystems **23:**65–76.

White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: a neglected concept in invasion biology. Diversity and Distributions **12:**443–455.