

BULLFROGS, DISTURBANCE REGIMES, AND THE PERSISTENCE OF CALIFORNIA RED-LEGGED FROGS

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Abstract: The introduction and spread of bullfrogs (*Rana catesbeiana*) in western North America may have played a central role in the declines of native ranid frogs. Specifically, a positive correlation exists between the absence of California red-legged frogs (*Rana aurora draytonii*) and the presence of introduced bullfrogs, but coexistence does occur in some environments. Enclosure experiments and diet studies have shown that bullfrogs prey on larval and juvenile California red-legged frogs. We used a modeling approach to quantify the threat of bullfrog predation on California red-legged frog populations. We created age-structured population models for both species. We used these models to (1) explore the sensitivity of red-legged frog populations to changes in the intensity of bullfrog predation; (2) explore the hypothesis that high flood frequencies increase the probability for coexistence in southern California streams; and (3) examine the efficacy of bullfrog management strategies, such as shooting adults and draining livestock grazing ponds. Our model simulations indicated that winter floods, which strongly increase mortality of bullfrogs but not red-legged frogs, facilitate coexistence if they occur more than once every 5 years. We found that increasing adult bullfrog mortality through shooting would benefit red-legged frogs only with extreme effort. Conversely, the draining of livestock grazing ponds can be effective in bullfrog management if draining occurs at least every 2 years. Shooting and draining in tandem were successful at decreasing bullfrog densities. Finally, our model provided a quantitative measure of bullfrog predation on California red-legged frogs that can potentially be used to assess the impact of bullfrogs on a site-by-site basis. Our model, plus experimental studies that link specific environmental factors to the bullfrog predation rate, can provide managers with a useful tool for controlling populations and facilitating conservation efforts for the California red-legged frog.

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Amphibians have suffered severe declines in the past 2 decades (Alford and Richards 1999). Several declines in the western United States have been associated with introduced aquatic predators (Moyle 1973, Bury and Luckenbach 1976, Fisher and Shaffer 1996, Knapp and Matthews 2000). Bullfrog introduction and spread in western North America have played a central role in the declines of several native ranid frogs (Moyle 1973, Bury and Luckenbach 1976, Schwalbe and Rosen 1988). Early surveys by Moyle (1973) found an abundance of bullfrogs in habitat formerly occupied by native frogs in California's southern central valley and suggested a causal relationship between bullfrog presence and the absence of native anurans. Several other experiments (Kiesecker and Blaustein 1997,

1998; Lawler et al. 1999; Christopher 2000; Kiesecker et al. 2001*b*), field studies (Fisher and Shaffer 1996), and observations have found that red-legged frog abundance is negatively correlated with the presence of bullfrogs.

The California red-legged frog is now extinct in approximately 70% of its historic range (Hayes and Jennings 1986, 1989; Jennings 1988; Jennings and Hayes 1994; Fisher and Shaffer 1996). Current working hypotheses to explain these declines include climate change, increased exposure to UV-B, and pesticides (Davidson et al. 2001), as well as historical overharvesting, habitat destruction, and introduced species (Jennings and Hayes 1985). These factors may work synergistically to decrease the California red-legged frog's chances for persistence (Hayes and Jennings 1986, Kiesecker et al. 2001*a*, Blaustein and Kiesecker 2002). Hence, it is difficult to determine the impact of introduced bullfrogs on red-legged frogs (Hayes and Jennings 1986, Kiesecker and Blaustein 1998, Lawler et al. 1999, Kiesecker et al. 2001*b*). Both

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species coexist in some environments, but red-legged frogs have become extinct in others (Hayes and Jennings 1986, Twedt 1993, Cook 1997, Christopher 2000). These observations form the basis for 2 fundamental questions: (1) can we determine which populations are more at risk of extinction because of bullfrog introductions? and (2) after identifying high-risk cases, what are the best options for bullfrog management?

The California red-legged frog and the bullfrog inhabit 2 distinct habitat types, ponds and streams. In southern California, streams periodically endure scouring floods. Because of natural history differences, these floods markedly decrease bullfrog populations but only slightly affect California red-legged frog populations (S. S. Sweet, University of California-Santa Barbara, personal communication). During peak flow, bullfrog larvae and adults remain in streams (Bury and Whelan 1984), while red-legged frogs are rarely seen along streams during this time (Rathbun et al. 1993; S. S. Sweet, University of California-Santa Barbara, personal communication). Because flooding events affect each species differently, flood frequency could influence the probability for coexistence of native California red-legged frogs with introduced bullfrogs in southern California streams.

Attempts to manage bullfrog populations have focused on both eradication of the larval stage and removal of adults (Rosen and Schwalbe 1995, Wassersug 1997, U.S. Fish and Wildlife Service 2002). The feasibility of managing bullfrogs from either adult or larval perspectives varies depending on location and habitat. For instance, drains can be installed in livestock grazing ponds, but draining larger wetlands is increasingly difficult and less beneficial for other wildlife.

Habitat type and location are both critical factors to consider when assessing bullfrog management options, particularly for the benefit of native anurans. Smaller artificial ponds can provide much-needed habitat for the California red-legged frog, but can become sinks when introduced bullfrogs are present (U.S. Fish and Wildlife Service 2002). Proposed pond management to benefit California red-legged frogs, when bullfrogs are present, includes regular and complete draining once every 3–4 years (U.S. Fish and Wildlife Service 2002). In habitats not amenable to hydroperiod alterations, attempts to eradicate bullfrogs have involved imposing large mortalities on adults via shooting (Schwalbe and Rosen 1988; Rosen and Schwalbe 1995; S. S. Sweet, University of California-Santa Barbara, personal communication).

Regardless of approach, successful bullfrog management will require much time and effort.

We used a mathematical model to explore consequences of bullfrog predation on California red-legged frog populations. We developed age-structured models for both frog species, and examined the effect of each model parameter on the overall population dynamics and persistence patterns. We examined the impact of floods and 2 bullfrog management strategies, the shooting of adult bullfrogs and the draining of livestock grazing ponds, on the population dynamics of both species and the persistence patterns for California red-legged frogs. By using a modeling approach, we addressed specific mechanisms that might underlie observed patterns of persistence. We assessed the effectiveness of different management strategies used to control bullfrog populations for the benefit of red-legged frog populations.

METHODS

The Basic Model

Many natural history aspects of the red-legged frog and bullfrog are similar, and the population models therefore share some key assumptions. Both species reproduce seasonally and have discrete, overlapping generations (Fig. 1). We used a yearly time step, with each new period starting at the beginning of April. We assumed a 1:1 sex ratio.

The red-legged frog breeds from late November to early April, and embryos hatch 6–14 days after fertilization (Stebbins 1985, Jennings 1988, Jennings and Hayes 1994). The tadpole stage is 6 months long, and metamorphosis typically occurs between July and September. Juveniles become sexually mature in 2–3 years. Adults can live up to 10 years (U.S. Fish and Wildlife Service 2002). Survival probabilities for the red-legged frog are for post-breeding census data. The first-year juvenile age-class combined both the tadpole and metamorph stages. We denoted 3 juvenile year classes $\{M_1, M_2, M_3\}$ and 1 adult stage class $\{C\}$ for red-legged frogs (Caswell 2001).

Bullfrogs living in the western United States breed from April to July (Bury and Whelan 1984, Stebbins 1985). We used pre-breeding census data for bullfrog survival probabilities. Tadpoles take 1 year to metamorphose, and juveniles reach sexual maturity in 2 years (Bury and Whelan 1984). We denoted 1 tadpole stage class $\{T\}$, 1 juvenile stage class $\{J\}$, and 1 adult stage class $\{A\}$ for bullfrogs (Caswell 2001).

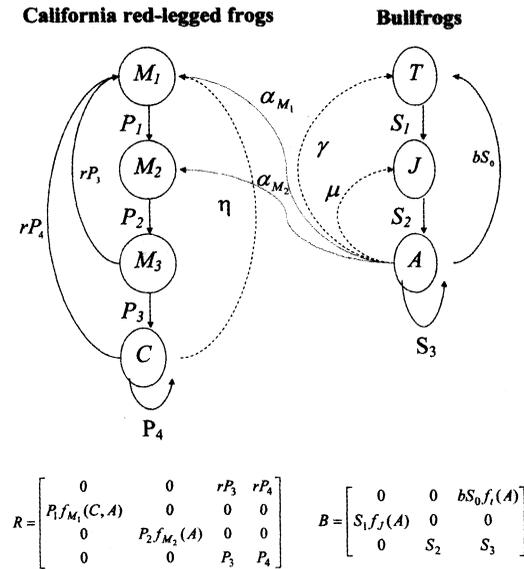


Fig. 1. Life-cycle diagrams and the corresponding population matrices for California red-legged frogs (R) and bullfrogs (B). In the life-cycle diagram, the solid arrows and corresponding parameters represent transitions between life stages and the survival probability for each transition. The dashed arrows and corresponding parameters represent cannibalism on tadpoles and juveniles by adults. The dotted arrows and corresponding parameters represent adult bullfrog predation on juvenile red-legged frogs. For the matrices, f_i represents losses due to predation and cannibalism on age class i ($i = T, J, A, M_1, M_2, M_3, C$). Survival probabilities between stage classes of red-legged frogs and bullfrogs, in absence of predation and cannibalism, are represented by P_i and S_i . Fecundity of red-legged frogs and bullfrogs is represented by r and b , respectively.

Bullfrogs are important predators in most aquatic ecosystems that contain red-legged frogs, but red-legged frogs are not an essential part of the bullfrog diet (Bury and Whelan 1984). In our model, bullfrog growth and reproduction was independent of red-legged frog consumption. Studies in the field and in artificial enclosures have shown that bullfrogs are capable of consuming red-legged frogs up to 75 mm in length (U.S. Fish and Wildlife Service 2002; Kiesecker and Blaustein 1997; S. V. Christopher, University of California-Santa Barbara, unpublished data). We assumed that adult bullfrogs have the largest impact on first- and second-year juvenile red-legged frogs, and included predation on only these 2 stages.

Cannibalism in bullfrogs is well documented in the field, and diet studies have found immature bullfrogs in the stomachs of adults (Bury and Whelan 1984, Schwalbe and Rosen 1988, Stuart 1993, Rogers 1996). Cannibalism also is known to occur in red-legged frog populations (N. J. Scott,

U.S. Geological Survey, personal communication). We assumed that adult bullfrogs eat both bullfrog tadpoles and first-year juveniles, and that adult red-legged frogs cannibalize only first-year juveniles.

Red legged frog population dynamics can now be written as:

$$\mathbf{v}(t + 1) = R\mathbf{v}(t). \tag{1a}$$

Bullfrog population dynamics can be written as:

$$\mathbf{u}(t + 1) = B\mathbf{u}(t), \tag{1b}$$

in which $\{\mathbf{v} = [M_1 \ M_2 \ M_3 \ C]'\}$ and $\{\mathbf{u} = [T \ J \ A]'\}$, are the population vectors for red-legged frogs and bullfrogs, respectively. The elements of each vector represent the density in each stage class (i.e., number of individuals/unit length of shoreline). The matrices R and B are the population matrices for red-legged frogs and bullfrogs, respectively (Fig. 1).

To derive functions for predation and cannibalism, we assumed that prey were caught at a rate proportional to the density of predators, and predator density remains constant within a time step, Δt . The fraction of bullfrog tadpoles $\{T\}$ that survived cannibalism is now written as the Ricker function (Gurney and Nisbet 1998):

$$f_T = \exp(-\gamma A(t)\Delta t), \tag{2}$$

where γ is the attack rate of adult bullfrogs foraging conspecific tadpoles. Using the same format, we derived functions for intraspecific predation on first-year juvenile bullfrogs

$$f_J = \exp(-\mu A(t)\Delta t), \tag{3a}$$

intraspecific and interspecific predation on first-year juvenile red-legged frogs

$$f_{M_1} = \exp((-\eta C(t) - \alpha_{M_1} A(t))\Delta t), \tag{3b}$$

and bullfrog predation on second-year juvenile red-legged frogs

$$f_{M_2} = \exp(-\alpha_{M_2} A(t)\Delta t), \tag{3c}$$

where attack rates are represented by μ (intraspecific predation on first-year juvenile bullfrogs), η (intraspecific predation on first-year juvenile red-legged frogs), and α_{M_1} and α_{M_2} (interspecific predation on first- and second-year juvenile red-

Table 1. Symbols and definitions for model parameters and the default values used in model simulations.

Parameter	Definition	Published value	Reference	Default mean parameter values	Parameter range for the annual variation
P_1	First-year juvenile red-legged frog survivorship	0.025	Licht 1974	0.0250	0.0225–0.0275
P_2	Second-year juvenile red-legged frog survivorship			0.250	0.225–0.275
P_3	Third-year juvenile red-legged frog survivorship	0.52	Licht 1974	0.40	0.36–0.44
P_4	Adult red-legged frog survivorship	0.686	Licht 1974	0.50	0.45–0.55
R	Red-legged frog fecundity ^a	1,000–3,000	Jennings and Hayes 1994	1,500	1,300–1,700
S_0	Bullfrog tadpole survivorship	0.12–0.18	Cecil et al. 1979	0.10	0.07–0.12
S_1	First-year juvenile bullfrog survivorship			0.020	0.015–0.025
S_2	Second-year juvenile bullfrog survivorship			0.32	
S_3	Adult bullfrog survivorship	0.65	Raney 1940	0.65	0.50–0.80
B	Bullfrog fecundity ^a	500–12,500	Bury and Whelan 1984	4,000	3,000–5,000
γ	Intra-specific attack rate on bullfrog tadpoles ^b			0.02	0.016–0.024
μ	Intra-specific attack rate on first-year juvenile bullfrogs ^b			0.05	0.04–0.06
η	Intra-specific attack rate on first-year juvenile red-legged frogs ^b			0.033	0.027–0.037

^a Fecundities have units of eggs/adult.

^b Attack rates have units of km shoreline cleared/adult/year.

legged frogs; Fig. 1; Table 1). All attack rate and cannibalism values have units of km shoreline cleared/predator/year.

We parameterized the model using published values when possible (Table 1). When values were unknown, we used values reported for closely related species. Values for survival probabilities have not been determined for either frog species in southern California, and those reported for the red-legged frog are for the northern subspecies, *Rana aurora aurora*. There are no published values for any of the cannibalism parameters. However, the cannibalism parameter determines the population's equilibrium density. To estimate reasonable values for the cannibalism parameters, we used densities of adult bullfrogs and red-legged frogs from field surveys and used those to solve for the cannibalism parameters.

Monte Carlo Simulations.—Considerable uncertainty existed in the values of all model parameters. To study the impact of this uncertainty, we ran 1,000 Monte Carlo simulations for both the deterministic and stochastic models (Monte Carlo Sets 1 and 2; Table 2). We selected parameter combinations at random from a symmetrical beta distribution bounded 40% above and below the default parameter values listed in Table 1. We only accepted parameter combinations that ensured population viability in the absence of predation (parameter combinations that yield eigenvalues for the population matrices ≥ 1). Following these simulations, we increased the degree of uncertainty by increasing the bounds on the sym-

metric beta distribution to 60% above and below the default parameter values.

Stochastic Simulations.—The environment that red-legged frogs and bullfrogs inhabit is complex and varies annually. To investigate effects of this variation, we organized the parameters into 3 groups: vital rates for the red-legged frogs, vital rates for bullfrogs, and attack rates describing cannibalism and predation. The parameter values within each group have a covariance of 1 (Table 2). We started simulations from the equilibrium population densities in the absence of predation and set the adult population density to zero if it dropped below 2 adult frogs/kilometer of shoreline. The extinction depended only weakly on the arbitrary value chosen to represent the adult extinction threshold.

Flooding Simulations

To simulate a year with a winter flood, we imposed additional mortalities on all bullfrog stage classes (excluding eggs) and all red-legged frog life stages (including eggs). We examined 3 extreme combinations of flood induced mortalities (Table 2). During flood years, we reduced survival probabilities for all bullfrog stage classes (excluding eggs) by 90, 80, or 70% and all red-legged frog life stages (including eggs) by 10, 20, or 30%, respectively. We explored persistence probabilities of red-legged frogs for a range of flood probabilities and attack rate values.

Historic Stream-Flow Simulations.— We inferred the natural flood frequencies for streams in Santa

Table 2. Names, descriptions, and details of each model simulation and uncertainty test.

Simulation	Description	Simulation details
Monte Carlo Set 1	Uncertainty in the default mean parameter values for the deterministic model	Parameter combinations were randomly chosen from a symmetrical beta distribution with upper and lower bounds set 40% above and below the default mean parameter values. We compare results for 1,000 random parameter combinations.
Stochastic Simulation	Annual variation in the vital rates and attack rates	Annual variation was incorporated by randomly choosing parameter values from a symmetrical beta distribution bounded 5% above and below the default mean attack rates and bounded 10% above and below the default mean vital rates from Table 1. We ran 1,000 realizations for each attack rate value ranging from 0–0.3.
Uncertainty Test 1	Uncertainty in the annual variation incorporated in the vital rates.	Same as the Stochastic Simulation described above except here the yearly variation in the vital rate parameters were randomly chosen from a symmetrical beta distribution bounded 40% above and below the default mean values. The same random numbers from the Stochastic Simulations were used for the annual variation in the attack rates. We ran 1,000 realizations for each attack rate value ranging from 0–0.3.
Uncertainty Test 2	Uncertainty in the annual variation incorporated in the attack rates	Same as the Stochastic Simulation described above except here the yearly variation in the attack rate parameters was randomly chosen from a symmetrical beta distribution bounded 40% above and below the default mean attack rate values. The same random numbers from the Stochastic Simulations were used for the annual variation in the vital rates. We ran 1,000 realizations for each attack rate value ranging from 0–0.3.
Monte Carlo Set 2	Uncertainty in the default mean parameter values for the basic stochastic model	We ran the Stochastic Simulation (1,000 realizations of the basic stochastic model) for each combination of mean parameter values used in the Monte Carlo Set 1. We fixed the annual variation by using the same random numbers from the original Stochastic Simulation.
Flood Simulation	Variation in flood frequencies	This simulation builds on the Stochastic Simulation described above. We ran the Stochastic Simulation for flood probabilities ranging from 0–0.4. We randomly select a flood year from a uniform distribution of random numbers ranging from 0–1 and impose additional flood mortalities of 80% on bullfrogs and 20% on red-legged frogs. We ran 100 simulations for each flood probability and predation attack rate.
Uncertainty Test 3	Uncertainty in the flood-induced mortality rates	We reran the Flood Simulation using flood induced mortality combinations of 70% bullfrogs/30% red-legged frogs and 90% bullfrogs/10% red-legged frogs.
Historic Flow Simulations	Simulations using the historic stream flow sequences	We ran the Flood Simulation described above only instead of randomly choosing flood years we used the historic flood sequence corresponding to streams in Santa Barbara and Ventura counties.
Adult Shooting	Shooting adult bullfrogs	This builds on the Stochastic Simulation by adding adult shooting mortalities of 0.3, 0.45, 0.55, 0.65, and 0.75, at frequencies ranging from once/yr to once/10 yr. We ran 100 realizations for each attack rate value ranging from 0–0.3 for each shooting mortality at each shooting frequency.
Pond Draining	Pond draining	This builds on the Stochastic Simulation by adding 100% mortality on the larval stage at intervals from once/yr to once/10 yr. We ran 100 realizations for each attack rate value ranging from 0 to 0.3 for each draining frequency.
Combination Treatment	The combination of shooting adult bullfrogs and pond draining	This simulation combines the adult shooting simulation with the pond-draining simulations. We imposed adult mortalities of 0.3, 0.45, 0.55, 0.65, and 0.75, with 100% tadpole mortality for frequencies of once/yr to once/10 yr. We ran 100 realizations for each attack rate value, adult mortality, and management frequency.

Barbara and Ventura Counties from historical stream-flow data of instantaneous peak flows. Our data came from sections of the Santa Ynez River, Sespe Creek, Matilija Creek, and Piru Creek (U.S. Geological Survey 2000). We combined this information with recorded observations of extreme disturbance to the streambeds and damage to adjacent roads (S. S. Sweet, University of California-Santa Barbara, personal communication; Road Damage Reports, U.S. Forest Service, Santa Barbara County, California). The February storms of 1992 were the lowest in intensity, yet caused damage to all of the streams previously mentioned. Therefore, we used the peak flows of these storms to define what constituted a flood year for previous and subsequent years.

The timing of bullfrog introductions, coupled with the unique flood sequence for each stream, may strongly influence the extinction probability for red-legged frogs. We used field notes and museum records to estimate the time of each introduction. Bullfrogs were first observed in Sespe Creek and Piru Creek in 1981 (S. S. Sweet, University of California-Santa Barbara, unpublished data). For Matilija Creek, the exact year is unknown. However, in the late 1940s, bullfrogs thrived at Mr. Lee's Frog Hatchery at Casitas Springs not far from Matilija (Sanders 1950). From this, we estimated that escaped bullfrogs were capable of establishing themselves in Matilija by 1950. The earliest museum record found for bullfrogs in the Santa Ynez River was May 1979, but they were most likely present before 1979. We ran 2 simulations for the Santa Ynez River, the first starting from 1979 and the second starting from 1969.

Bullfrog Management

Adult Shooting.—We measured effort in 2 ways: the additional mortality imposed on the adult bullfrog population and the period of each shooting event. The additional mortality was multiplicative. For example, an additional mortality of 30% means that adult year-to-year survival is reduced to 70% of its previous value. We examined effects of additional mortalities of 30, 45, 55, 65, and 75%, for shooting frequencies ranging from 0.1 to 1 (a shooting frequency of 0.1 corresponds to imposing an additional mortality on adult bullfrogs once every 10 years).

Pond Draining.—We used the basic model described previously in this section, but induced 100% mortality in the tadpole life stage of bullfrogs to simulate the effects of pond draining. We varied the draining period (number of years

between each pond draining event) from 0.1 to 1 (a pond draining frequency of 0.1 corresponds to draining a pond once every 10 years).

The Combined Management Strategy of Pond Draining and Adult Shooting.—After examining the effect of imposing an additional adult mortality and eliminating a cohort of tadpoles separately on the population dynamics of bullfrogs and the persistence patterns of red-legged frogs, we explored simulations combining both strategies. We simultaneously imposed an additional adult mortality of 30, 45, 55, 65 or 75%, and a tadpole mortality of 100% over a range of frequencies from 0.1 to 1.

Model Analysis

The model described in this section is complex (multispecies, multi-age classes, and several types of stochasticity). We first studied a number of simplified, deterministic models more amenable to formal mathematical analyses, whereby a secure conceptual foundation was provided for the interpretation of large computer simulations. We calculated the equilibria of the simplified models, and reported the results of each simulation and tests of uncertainty (Table 2).

RESULTS

Equilibria, Stability, and Uncertainty

Single Species Red-legged Frog Equilibrium Analyses.—With cannibalism, but without predation, we have 2 independent density-dependent models. The model for red-legged frogs describes the dynamics of a red-legged frog population in a system that has not been invaded by bullfrogs. From equations 1a and 3b, equilibria densities for each stage class can be calculated. The density of adult red-legged frogs in equilibrium is

$$C^* = \frac{1}{\eta \Delta t} \ln \left[\frac{r P_1 P_2 P_3}{1 - P_4} \right]. \quad (4)$$

This indicates a viable equilibrium, provided that fecundity can compensate for background mortality in the stage classes (i.e., $r \geq [1 - P_4] / P_1 P_2 P_3$). The equilibrium density approaches zero as the cannibalism attack rate parameter, η , becomes very large, but the population cannot become extinct purely because of cannibalism. The parameter η merely controls the equilibrium population size.

Because the expression for cannibalism is of the Ricker type, the equilibrium may be stable or unstable, depending on parameter values (Gurney and Nisbet 1998). With unstable equilibria, long-

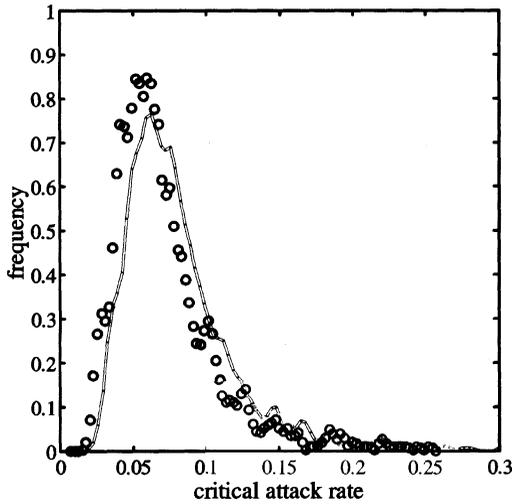


Fig. 2. A large variation in the default parameter values in Table 1 results in a narrow distribution of critical attack rates (the bullfrog predation rate beyond which red-legged frogs will become extinct; units are in km shoreline cleared/adult bullfrog/yr). Little difference exists between the distribution for the deterministic model (solid line) and the stochastic model (circles).

term population dynamics may be oscillatory or chaotic. With the default parameters in Table 1, equilibria can be shown to be invariably stable.

Single-Species Bullfrog Equilibrium Analyses.—Equilibrium densities for bullfrog stage classes can be calculated from equations 1b, 2, and 3a. The density of adult bullfrogs in equilibrium is

$$A^* = \frac{1}{(\gamma + \mu)\Delta t} \ln \left[\frac{bS_0S_1S_2}{1 - S_3} \right], \quad (5)$$

and is positive provided that $b \geq (1 - S_3) / S_0S_1S_2$. The parameters μ and γ control the equilibrium population size, which approaches zero as these parameters become very large. Equilibria are stable with the default parameters in Table 1. A large change in the parameter values is required before getting unstable equilibria. Unstable equilibria results in oscillations with a period of approximately 4 years. This corresponds to the time one cohort takes to pass through all of the life stages.

Two-Species Equilibrium Analysis.—We analyzed the 2-species deterministic version of our model that includes both intraspecific and interspecific predation. Equilibrium densities for red-legged frog stage classes can be calculated from equations 1a, 3b, 3c, and 5 (bullfrog equilibrium densities do not change). The density of adult red-legged frogs in equilibrium is

$$C^* = \frac{1}{\eta\Delta t} \ln \left[\frac{rP_1P_2P_3}{1 - P_4} \right] - \frac{\alpha_{m_1} + \alpha_{m_2}}{\eta(\gamma + \mu)\Delta t} \ln \left[\frac{bS_0S_1S_2}{1 - S_3} \right]. \quad (6)$$

The population will go extinct with $C^* \leq 0$. This equation implies that red-legged frogs and bullfrogs can coexist provided that

$$\alpha_{m_1} + \alpha_{m_2} \leq \frac{(\gamma + \mu) \ln \left[\frac{rP_1P_2P_3}{1 - P_4} \right]}{\ln \left[\frac{bS_0S_1S_2}{1 - S_3} \right]}. \quad (7)$$

We refer to $\alpha_{M_1} + \alpha_{M_2}$ as the predation attack rate, and to the highest attack rate allowing for coexistence as the critical attack rate. With the default parameters in Table 1, the critical attack rate is 0.071 km shoreline cleared/adult bullfrog/year.

Monte Carlo Set 1.—We investigated the sensitivity of the critical attack rate by calculating the critical attack rate value using equation 7 for randomly chosen parameter values as described earlier (Monte Carlo Set 1; Table 2). Large variations in the parameter values resulted in a narrow distribution of critical attack rates (Fig. 2). Increasing the uncertainty in the bullfrog parameters increased the frequency of larger critical attack rate values. Increasing the uncertainty in the red-legged frog parameters increased the frequency of smaller critical attack rate values.

Stochastic Simulations.—Adding year-to-year variation created fluctuations around the equilibrium density more closely resembling natural population dynamics (Fig. 3a). The results of the stochastic simulation revealed that these fluctuations lead to a distribution of attack rates that may cause extinction and a decrease in the critical attack rate to approximately 0.0616 (Fig. 4a). The critical attack rate for the stochastic simulations corresponds to 50% extinction after 100 years (Fig. 4a).

Uncertainty Tests 1 and 2.—For examining the results of uncertainty in yearly variation (Uncertainty Tests 1 and 2; Table 2), we compared the width of the 5 and 95% extinction isoclines (Fig. 5a). From the first and second uncertainty tests (Table 2), we found that increasing the yearly variation in vital rates widens the range of attack rates above and below the critical attack rate value, in which extinction is possible (i.e., increases the distance between the 5 and 95% extinction curves). Increasing the yearly variation in the cannibalism and attack rates has little effect on this interval.

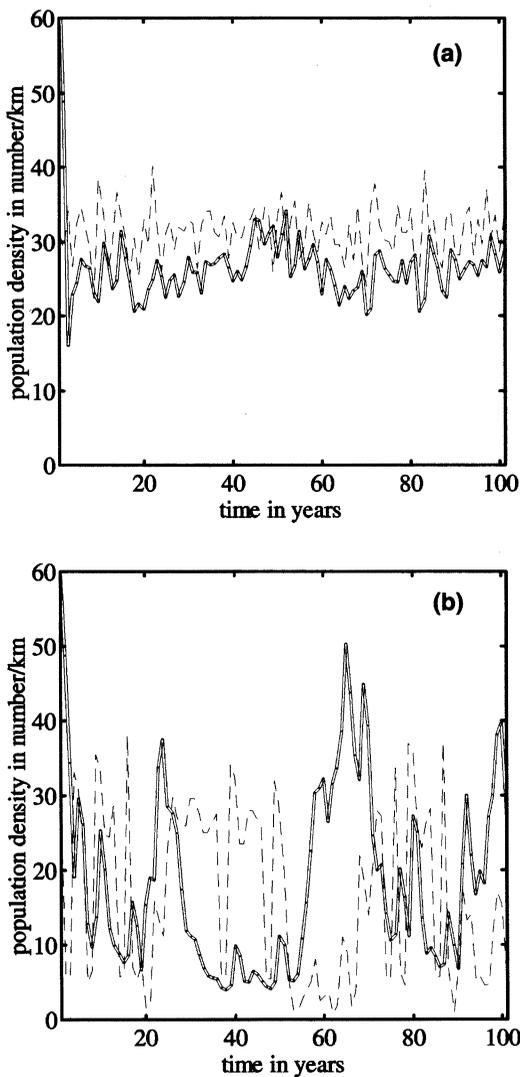


Fig. 3. (a) A sample realization from a stochastic simulation showing coexistence of red-legged frogs (solid line) with bullfrogs (dashed line). (b) A sample realization from a flood simulation with a flood probability of 0.25/yr. The incorporation of periodic floods induces volatility in the dynamics of both the red-legged frog (solid line) and bullfrog (dashed line) populations.

Monte Carlo Set 2.— The results of the Monte Carlo Set 2 (Table 2) revealed that uncertainty in the mean parameter values also had no effect on this extinction interval. However, changes in the mean parameter values altered the critical attack rate value by shifting the graph (Fig. 4a) along the attack rate axis (Fig. 5a). Because little variation exists in the width of the 5–95% extinction isoclines, the critical attack rate value becomes

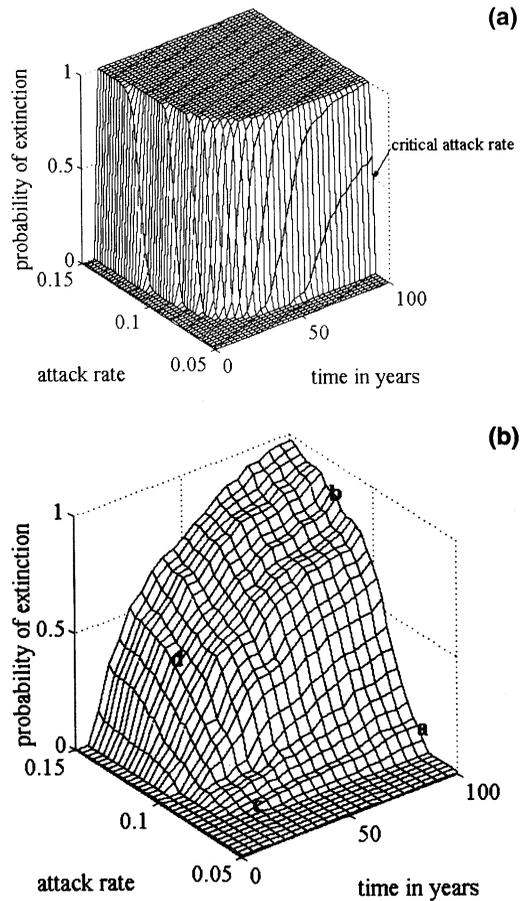


Fig. 4. The extinction probability for red-legged frogs varies with time and with the bullfrog attack rate (in km shoreline cleared/adult bullfrog/yr). (a) For the Stochastic Simulation with only interannual variation in default parameter values, a narrow distribution of attack rate values results in a range of extinction probabilities ranging from 0–100% for any given year. The attack rate value corresponding to a probability of extinction of 50% after 100 years represents the stochastic critical attack rate value. (b) For the Flood Simulation, the range of attack rates has greatly increased, and overall the probability of extinction has decreased (flood probability of 0.3/yr). Labels (a–d) correspond to graphs a–d in Fig. 6.

useful for measuring effects of uncertainty. As with the deterministic model, a large variation in the parameter values, results in a narrow distribution of critical attack rates (Fig. 2).

Flooding Simulations

Following a single flood year, the bullfrog population exhibits overcompensatory oscillations. The overcompensation is initially caused by a strong decrease in cannibalism at low adult bullfrog densities, yielding a high number of juvenile

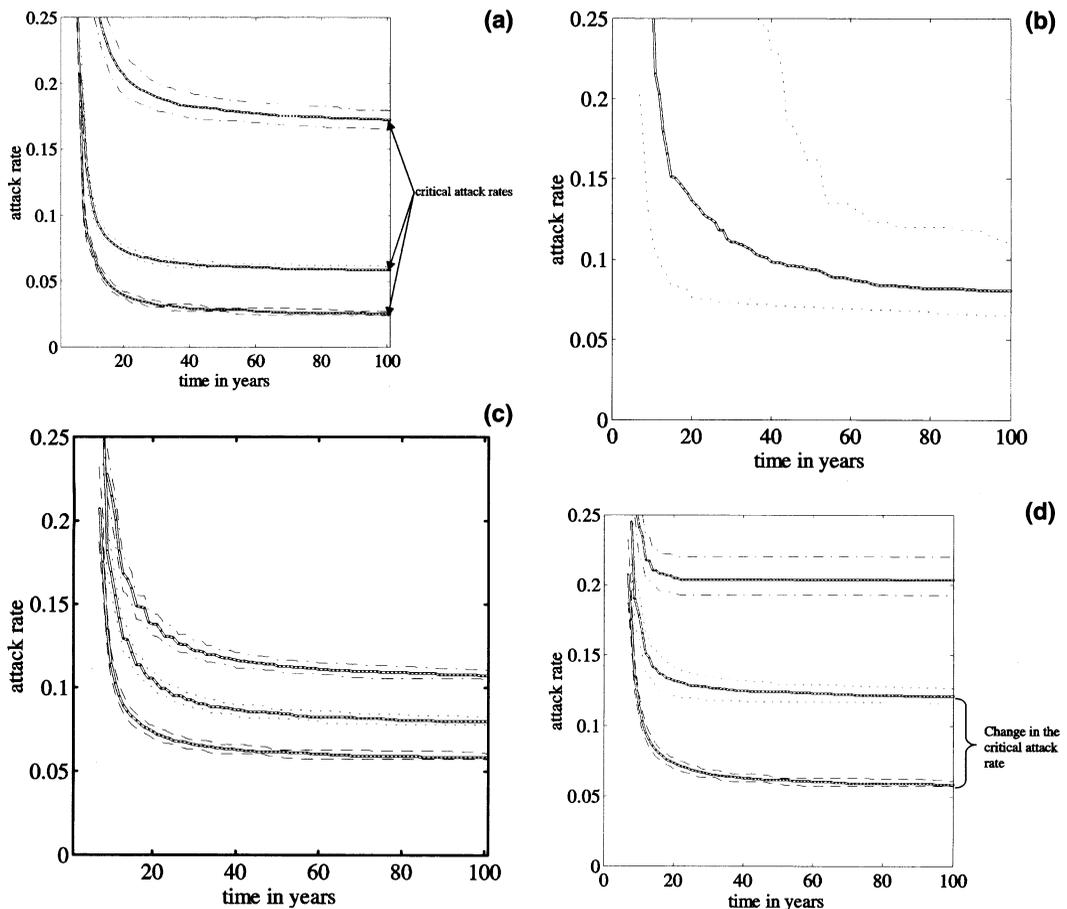


Fig. 5. The effect of changes in the mean parameter values, flooding and bullfrog management strategies, on red-legged frog persistence is best illustrated by graphing the 5, 50, and 95% extinction probabilities over the range of attack rate values and time period used in model simulations. The values corresponding to a 5 and 95% extinction probability are represented by the broken lines above and below the solid line. The solid line represents the values corresponding to a 50% extinction probability. We refer to this curve representing the probability of extinction as an isocline curve. (a) Uncertainty in the default vital rates and cannibalism parameters result in a small difference in the width of the 5 and 95% isocline curves relative to the 50% curve. Instead, we see a shift in the position of these curves along the attack rate axis. This shift results in a change in the stochastic critical attack rate. The first graph (a) shows simulations with a critical attack rate of 0.0289 (dashed line), 0.0616 (the default parameter values, dotted line) and 0.1785 (dotted and dashed line). (b) Incorporating random floods into the model has a different effect on the shape of the isocline curves. Random flooding increases the width and variability of the 5 and 95% isocline curves with respect to the 50% isocline curve (flood probability of 0.3/yr). (c) and (d) Incorporating bullfrog management strategies does not change the width of the 5 and 95% isocline curves relative to the 50% curve and like the effects of parameter uncertainty, simulations of bullfrog management strategies result in a shift in the position of the isocline curves along the attack rate axis. This shift in the 50% isocline curve corresponds to a change in the critical attack rate (as illustrated in d). (c) Isocline curves from simulations corresponding to the management strategy of increasing adult bullfrog mortality by an additional 75% with a shooting frequency of every year (dotted-dashed lines), every other year (dotted lines) and every 5 years (dashed lines). (d) Isocline curves from simulations corresponding to the management strategies of increasing bullfrog tadpole mortality by draining ponds once every 2 years (dotted lines) and the combination of draining ponds and shooting adults every 2 years with an additional adult mortality of 30% (dotted-dashed lines). The lowest curve (dashed lines) corresponds to the simulation using the default parameter values without managerial intervention.

bullfrogs. When this cohort of juveniles becomes adults, they impose a strong cannibalism pressure on the subsequent cohorts of juveniles. This alteration of undershoots and overshoots eventually fades since the equilibria are stable. With high flood recurrence, bullfrog population dynamics

become very volatile, leading to a decrease in the mean adult bullfrog density. This in turn increases the mean red-legged frog density, but their population dynamics also become very volatile.

We investigated persistence patterns for red-legged frogs as a function of flood probability and

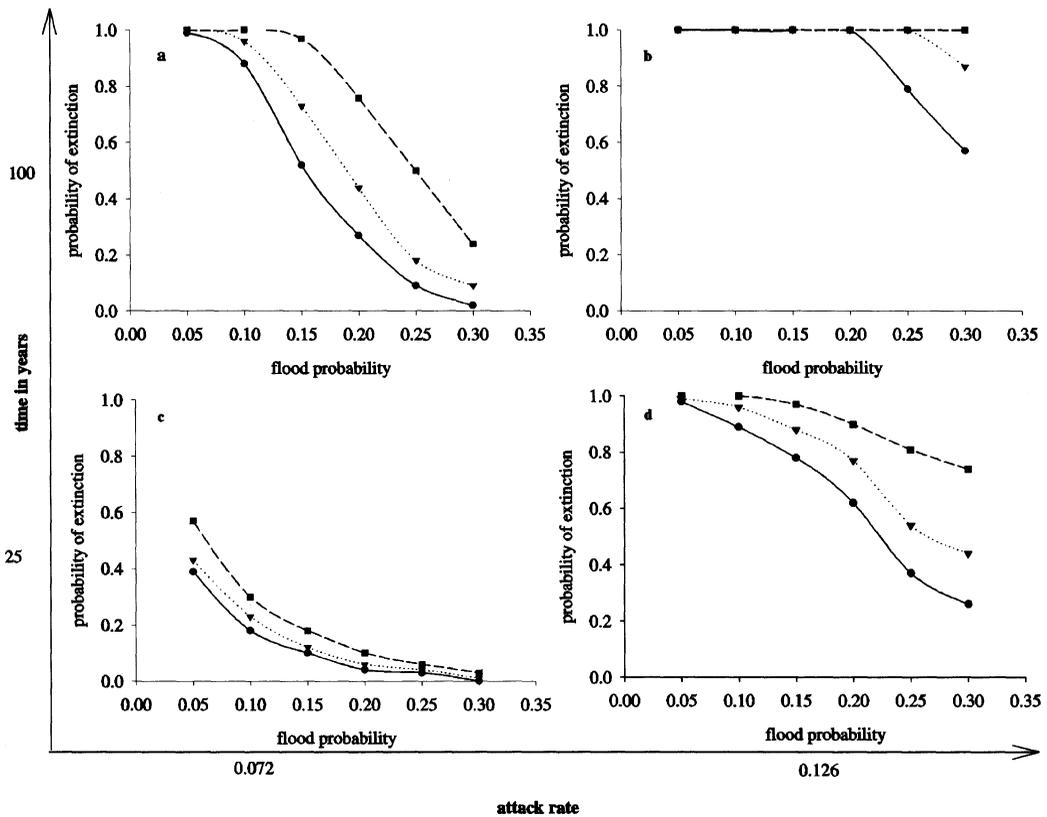


Fig. 6. A large decrease in the probability of extinction occurs after incorporating the effect of floods into model simulations. The magnitude of this decrease depends on the probability of a flood, its impact on mortality, the bullfrog attack rate parameter, and the time since bullfrog introduction. Each graph illustrates the effect of selected combinations of flood-induced mortalities (90 and 10% [■], 80 and 20% [▼], and 70 and 30% [●] for the bullfrogs and red-legged frogs, respectively) on the probability of extinction as a function of flood probability for the following combinations of time since a bullfrog introduction (yr) and attack rate (km shoreline/adult bullfrog/yr): (a) 100 and 0.072; (b) 100 and 0.126; (c) 25 and 0.072; (d) 25 and 0.126. Graphs (a–d) correspond to labels a–d in Fig. 4b.

attack rate. The probability of a flood decreases the density of adult bullfrogs and therefore increases the range of attack rates for which coexistence is possible. With this, the probability of extinction for red-legged frogs decreased with increasing flood probability (Figs. 4a, 4b).

Uncertainty Test 3.—Incorporating floods into the model at random had a large effect on the width of the 5–95% extinction interval (Fig. 5b), making the critical attack rate value a less reliable measure of the effects of uncertainty in the flood induced mortality rates. The effect that uncertainty in flood-induced mortality rates had on the model’s ability to predict probability of extinction for red-legged frogs was largely dependent on flood probability, bullfrog attack rate, and time since bullfrog introduction (Fig. 5a–d). The results of uncertainty test 3 (Table 2) revealed

that for attack rates close to the critical value, the model predictions for short-term persistence (approx 25 years) were relatively robust, but predictions for long-term persistence (closer to 100 years) were not (Fig. 5a–d).

Historic Stream-Flow Simulations.—Bullfrogs were present in all streams of interest for at least 20 years prior to our study. Therefore, we calculated the attack rate corresponding to 50% extinction after 20 years. We refer to this value as the 20-year critical attack rate. We ranked each stream by the change in the 20-year critical attack rate from that calculated in simulations without floods (Fig. 4a). The watersheds ranked as follows: the 2 sections of the Santa Ynez River (97 and 59% increases in 20-year critical attack rate), Sespe Creek (47%), Piru Creek (45%), and Matilija Creek (10%). We checked our results using the other disturbance mortality values

(Table 2) and found differences in the actual values of the 20-year critical attack rate, but the ranking between the watersheds did not change.

We ran 2 simulations for the Santa Ynez River: 1 corresponding to a bullfrog introduction in 1979 and 1 corresponding to a bullfrog introduction in 1969. For the section of the Santa Ynez River between Gibraltar Reservoir and Lake Cachuma, the percent increase in the 20-year critical attack rate dropped to 27 from 59%. Conversely, the section of the Santa Ynez River between Jameson Lake and Gibraltar Reservoir increased slightly to 105 from 97%.

Bullfrog Management

Adult Shooting.—Imposing additional mortality on adult bullfrogs every year or every other year, decreased the equilibrium population density in line with equation 5. Shooting frequencies greater than every other year caused fluctuations in the bullfrog population, with larger shooting mortalities resulting in larger fluctuations. This is a result of the overcompensatory population dynamics due to cannibalism as described in the previous section. These fluctuations in the population dynamics correspond to the shooting frequency, with the exception of every 4 years. A shooting frequency of every 4 years magnifies the natural oscillations that can occur when the bullfrog population dynamics are unstable and corresponds to the time it takes for a cohort to pass through all of the life history stages. In cases of large oscillations and persistence, the red-legged frog population dynamics converge, or oscillate synchronously, with that of the bullfrogs.

Similar to our analysis with floods, we examined the likelihood of coexistence for red-legged frogs as a function of the shooting frequency and the predation attack rate. The width of the 5–95% extinction curves remained the same for all shooting frequencies and mortalities (Fig. 5c). Therefore, we used the critical attack rate value as a yardstick to measure the effectiveness of each management regime. Adult-shooting mortalities of 75% at 1- and 2-year shooting intervals resulted in a 79 and 40% increase in the critical attack rates, respectively. Similarly, adult-shooting mortalities of 65% at 1- and 2-year shooting intervals resulted in a percent increase in the critical attack rates of 67 and 34%, respectively. Intervals ≥ 2 years or mortalities $\leq 65\%$ had small effects on persistence patterns for red-legged frogs.

Pond Draining.—The consequence of pond draining was the complete annihilation of a bull-

frog generation. This caused oscillations in the bullfrog population similar to, but smaller than, those caused by adult shooting. In cases of coexistence and large oscillations, the red-legged frog population dynamics synchronized with the bullfrog population. In model simulations, we did not allow bullfrog immigration from outside sources. Hence, pond draining every year drove the bullfrog population extinct within 10 years. Pond draining every 2 years decreased the mean bullfrog population density from 30 to 15 adults/km of shoreline and resulted in a 101% increase in the critical attack rate (Fig. 5d). Draining frequencies ≤ 2 years had little to no effect on the persistence of red-legged frogs.

The Combined Management Strategy of Pond Draining and Adult Shooting.—The management strategy of imposing additional mortalities on both adults and tadpoles in tandem with a frequency of once per year drove bullfrog populations extinct within 10 years. When tadpole mortality of 100% and adult mortality of 75, 65, and 55% was imposed on bullfrog populations every 2 years, bullfrogs were extirpated within 15, 25, and 40 years, respectively. Implementing pond draining and adult bullfrog mortalities of 45 and 30% every 2 years decreased the mean bullfrog population density from 30 to 3 and 6 adults/km of shoreline, and resulted in a 381 and 235% increase in the critical attack rate (Fig. 5d).

DISCUSSION

Parameter Uncertainty

Much uncertainty existed in our parameter values. Through simulations explicitly addressing uncertainty, we found that changes in the mean parameter values affected the quantitative predictions of the model but had little effect on the direction of model predictions. For example, using a different set of mean parameter values for the adult shooting simulation changes the exact attack rate value, but does not alter the change in the attack rate value resulting from the imposed management strategy. As such, our model predictions are robust despite the uncertainty associated with parameter values. This is important because the main purpose of this modeling effort was to evaluate the relative effectiveness of management options. Parameter values will vary among regions and habitats, and obtaining careful estimations of every parameter value is time-consuming and in some cases impossible. Conversely, obtaining estimates of a few key

parameter values and understanding how they vary across regions and habitat types is more amenable to field manipulations and can be more informative than excellent approximations of all parameters for a single study area.

Disturbance Regimes

The likelihood of extinction for red-legged frogs in model simulations was largely influenced by the flood frequency. Our model simulations show that flood frequencies $\geq 0.2/\text{year}$ can facilitate the persistence of red-legged frogs. Simulations using the historic stream flow records revealed that coexistence was also determined by the exact sequence of flood years (i.e., the flood sequence), particularly within the first 10 years after a bullfrog introduction. We ran 2 simulations for the Santa Ynez River: 1 corresponding to a bullfrog introduction in 1979 and 1 corresponding to a bullfrog introduction in 1969 and found striking differences in the percent increase in the 20-year critical attack rate. We found a significant difference in the flood sequence in the first 10 years between simulations starting in 1969 as opposed to 1979. Similarly, after 1978, Matilija Creek had the exact flood sequence found in the first section of the Santa Ynez River but had the lowest ranking. The mechanism behind Matilija's low ranking was a large gap between the first flood year (1952) and the second flood year (1969) after a bullfrog invasion introduction. These 2 simulations reveal that the flood sequence within the first 10 years after a bullfrog introduction is a critical window dictating the outcome of coexistence versus extinction.

Bullfrog Management

Efforts taken to eradicate bullfrog populations by increasing adult mortality through shooting are likely to be ineffective in promoting coexistence. First, a large amount of effort, a mortality of 65% or greater every 2 years, is required to make shooting adults beneficial for red-legged frog persistence. Second, this effort can create fluctuations in bullfrog population dynamics, which in turn may cause large fluctuations in the red-legged frog population. These fluctuations would make red-legged frog populations more vulnerable to extinction. However, these fluctuations are a product of the Ricker function used for density dependence. Presently, we do not have sufficient data on population dynamics to rigorously test mechanisms creating density dependence in fullfrog populations. In our

model, we assume cannibalism, and, unfortunately, this mechanism cannot be tested directly without prohibitive effort. However, Rosen and Schwalbe (1995) conducted intense bullfrog removal experiments in the San Bernardino National Wildlife Refuge, Cochis County, Arizona, and saw populations rebound to 50–80% of pre-removal densities within 3–4 months. This large rebound in adult densities is in line with population dynamics predicted by our model. In a similar field experiment, large rebounds in the adult population was observed following a shooting year along the Sespe Creek drainage near Rose Valley, Ventura County, California (S. S. Sweet, University of California-Santa Barbara, unpublished data). Studies of transient responses suggest the nature of density dependence, in particular the presence or absence of the overcompensation implied by our Ricker function.

The population response to pond draining was subdued in its oscillations, and the results of model simulations showed that pond draining can facilitate the coexistence of red-legged frogs with bullfrogs if done at least every 2 years. In contrast, the 2002 Recovery Plan for the California Red-legged Frog recommended an interval of 3–4 years. In our model, pond draining every 2 years successfully reduced bullfrog population densities by 50%. Draining frequencies less than once every 3 years had little effect on bullfrog densities, and, in turn, red-legged frog persistence. Unfortunately, our model did not incorporate bullfrog immigration or emigration; we realize this is an unrealistic assumption, as bullfrogs are excellent dispersers. Therefore, we suggest that ponds in close proximity (5–10 km) be managed as 1 large collective and precautions be taken to decrease immigration from nearby rivers. In most cases, ponds prove to be the source population for nearby rivers and streams, so managing the pond sources may help to decrease bullfrog populations elsewhere.

The combination of shooting adults and draining livestock grazing ponds was extremely more successful at eliminating bullfrogs than either strategy independently. Even low shooting efforts significantly decreased adult bullfrog densities by 80% when coupled with pond draining. Higher shooting efforts successfully eliminated bullfrog populations.

Understanding Attack Rate

Research has revealed that amphibian declines are the result of multiple factors working synergistically (Blaustein and Kiesecker 2002). The key insight from our basic model is the role of the

attack rate in determining coexistence versus extinction. Thus, it is important to understand how attack rate interacts with other causes of decline, such as habitat destruction and the presence of other introduced predators.

The attack rate is a measure of bullfrog search efficiency. Specifically, attack rate measures the average length of shoreline that is kept clear of prey items by a bullfrog in a given time interval. We expect the attack rate to be strongly influenced by habitat complexity, with more complex shorelines producing lower attack rates. Conversely, habitats that are highly modified by human activity, typically characterized by a decrease or complete lack of habitat complexity, we expect to have high attack rates. In other words, we expect bullfrogs to be less efficient at keeping a complex shoreline—choked with cattails and bulrushes clear of prey items—then they would be a shoreline devoid of such vegetation.

The original motivation behind this modeling work came from the observation that both species coexist in some environments, but not in others (Hayes and Jennings 1986, Twedt 1993, Cook 1997, Christopher 2000). Field observations documenting coexistence and extinction support our hypothesis as to how the attack rate changes with habitat complexity. Field observations documenting coexistence are within large marshes and ponds with high habitat complexity (Twedt 1993, Cook 1997, Adams et al. 1998, Christopher 2000). Twedt (1993) attributed the coexistence of bullfrogs and red-legged frogs to differences in microhabitat use, which would decrease the attack rate. California red-legged frogs also occupy and breed in artificial and highly modified habitats, such as livestock grazing ponds and reservoirs. However, they do not occur in these habitats when bullfrogs are present (Davidson et al. 2001). Cattle effectively trample all emergent vegetation growing within and around the perimeter of a pond or stream, thus greatly decreasing habitat complexity (Gunderson 1968, Kauffman and Krueger 1984). In addition to livestock, changes in wetland hydrology, from ephemeral to permanent, and the regulation of flow regimes also decrease the structural complexity of habitats (Richter and Azous 1995, Poff et al. 1997, Adams 1999). Habitat destruction has obscured our ability to directly assess the effects of introduced predators on the overall declines of red-legged frogs (Hayes and Jennings 1989; Adams 1999, 2000; Davidson et al. 2001). This model, plus experimental studies linking specific

environmental factors to the attack rate parameter, can be used to disentangle the correlated factors of habitat destruction and introduced bullfrogs and help to understand how these 2 factors work synergistically to eliminate red-legged frogs.

Along with habitat destruction, predation pressure from other introduced predators, such as fish, red-swamp crayfish (*Procambarus clarkii*), and signal crayfish (*Pacifasticus leniusculus*), have hampered our ability to directly assess the threat of introduced bullfrogs (U.S. Fish and Wildlife Service 2002). The impacts of these other predators are a large decrease in survivorship of eggs and larvae, and possibly a decrease in juvenile and adult survivorship (Kiesecker and Blaustein 1998, Lawler et al. 1999). In cases of overlap between introduced fish, crayfish, and bullfrogs, a much lower bullfrog attack rate would suffice to rapidly eliminate red-legged frogs. Under these circumstances, actions should be taken to control the densities of both bullfrogs and introduced fish and crayfish. Pond draining can successfully accomplish this. In addition, evidence suggests that frequent winter floods, typical of California streams, can hinder the invasion success of fish native to eastern North America (Fausch et al. 2001). Thus, flood disturbance regimes used to manage bullfrog populations, flood frequencies $\geq 0.2/\text{year}$, also may apply to reduce introduced fish populations.

MANAGEMENT IMPLICATIONS

Our model evaluates the sensitivity of red-legged frog populations to bullfrog predation, the role of flood regimes in facilitating coexistence in rivers and streams and the relative effectiveness of bullfrog management options on increasing the likelihood of coexistence. The construction of dams and reservoirs has altered the hydrologic regimes of most rivers and streams in southern California (Poff et al. 1997, Richter et al. 1997). We now have means of controlling flow regimes downstream of these sites (Fausch et al. 2001). Managers can use this control to the advantage of red-legged frog conservation by manipulating flows to favor native frogs and decrease bullfrog densities.

Our model suggests that the combination of shooting adults and draining ponds will be the most successful bullfrog management strategy. Eliminating bullfrogs by the removal of adults alone would require an exorbitant amount of effort. However, the low level of adult mortality required for the combined treatment to render effective lends to the argument that simply

removing bullfrog take limits in non-native areas could work synergistically with pond draining efforts to facilitate coexistence. Any effort to successfully eradicate bullfrogs would be time-consuming and costly, but maintaining bullfrog population densities below a critical level is feasible. Estimating a critical bullfrog density would require better estimates of the attack rate, including a better understanding of how the attack rate varies with habitat complexity.

Environmental variability plays a large role in invasion success. Thus, predicting the outcome of an exotic species invasion and the impact that species will have on the native biota is difficult (Moyle and Light 1996a,b). Interactions among several factors, including stochastic events, have more than likely played a role in eliminating red-legged frogs from certain regions but not others. Quantifying the effect of introduced bullfrogs on red-legged frogs is difficult. Undoubtedly, their role varies on a site-by-site basis. From our model, we have a quantitative measure of bullfrog predation on California red-legged frogs that can potentially be used to assess individual sites. Our model, plus experimental studies that link specific environmental factors to the attack rate parameter, can provide managers with a useful tool for controlling bullfrog populations and facilitating the conservation efforts for the California red-legged frog.

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