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MATRIX MODEL INVESTIGATION OF INVASIVE SPECIES CONTROL: BULLFROGS ON VANCOUVER ISLAND

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Abstract. Invasive species control is now a conservation priority in many parts of the world. Demographic modeling using population matrix models is a useful tool in the design of these control efforts as it identifies the life stages with the strongest influence on population dynamics. As a case in point, American bullfrogs (*Rana catesbeiana*) have been introduced around the world and have negative effects on native fauna. We studied demography of four populations on southern Vancouver Island, Canada, using field observations and capture–mark–recapture methods to estimate survival, growth, and fecundity. The life cycle of these introduced bullfrogs progressed in yearly increments through the following stages: eggs/small tadpoles, first-year tadpoles, second-year tadpoles, metamorphs/juveniles, and adults. Some bullfrog tadpoles were able to skip the second-year tadpole stage and metamorphosed one year after hatching. With tadpole survival estimates from the literature and field estimates of the remaining parameters we constructed a matrix population model. Prospective demographic perturbation analysis showed that bullfrog population growth rate (λ) was most influenced by the proportion of tadpoles metamorphosing early (tadpole development rate), and by early postmetamorphic survival rates. Most current control efforts for bullfrogs have focused on removing tadpoles and breeding adults, and our modeling suggests that these efforts may not be optimal. Partial removal of tadpoles may lead to higher tadpole survival and development rates and higher postmetamorphic survival due to decreased density-dependent competition. Removal of adults leads to higher survival of early metamorphic stages through reduced cannibalism. Our modeling suggests that culling of metamorphs in fall is the most effective method of decreasing bullfrog population growth rate. Our study shows how demographic information can be used to maximize the efficacy of control efforts, and our results are likely directly applicable to other invasive species with complex life cycles.

Key words: amphibian demography; capture–mark–recapture; complex life cycle; elasticity; introduced species; invasive species control; loop analysis; population growth rate and matrix models; Rana catesbeiana; *sensitivity; survival rate.*

Introduction

Introduced species are now recognized as a grave threat to native flora and fauna and the need to design effective control of their spread is increasing (Dolan et al. 2003). These control efforts are often based on the ease of implementation and usually target only part of the life cycle of the introduced species. Targeting one or the other life stage could have very different effects on population growth rate, especially if the introduced species exhibits a complex life cycle and the life stages occupy diverse ecological niches. Control efforts should therefore be assessed both in terms of their effect on overall population growth and in relation to logistical ease of implementation. Population projection matrices can be used to examine how the population growth rate would be affected by changes to vital rates brought about by alternate control measures (Lampo and De Leo 1998, McEvoy and Coombs 1999, Parker 2000). They can also be used to set target reductions in vital rates necessary to effect the desired decrease in population growth rate. The feasibility of achieving these targets can then be evaluated with respect to logistical ease of implementation and cost. Matrix population models have been used to predict the effectiveness of biocontrol agents, which may target specific life stages of a pest species (Shea 1998). Here we argue that they are also useful to evaluate management options for the control of introduced species with complex life cycles, where different methods may be required to control individual life stages (see also Lampo and De Leo 1998).

American bullfrogs (*Rana catesbeiana*) have been widely used in the farming of frog legs for the gourmet market. These frogs have escaped or been released from these farms and have established feral populations in many parts of the world. Introduced bullfrogs have negative effects on native fauna (Moyle 1973, Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et

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TABLE 1. Characteristics of the four study ponds in southern Vancouver Island, British Columbia, Canada.

Pond	Pond size (ha)	Population density (no./ha)†	CMR‡ duration	No. captured	No. recaptured§	Frog mass (g)
Beaver Pond	0.334	230 (100)	1998–2003	391	77	116.4 (84.8)
Copley Pond	0.0255	390 (98)	1998–2003	56	25	272.0 (113.1)
Trevlac Pond	2.96	29 (1.1)	1999–2003	242	35	143.9 (106.3)
Prior Lake	5.92	8.8 (4.4)	1999–2002	557	54	101.2 (84.3)

Note: Values in parentheses following means are SD.

† Population density of juvenile and adult bullfrogs is expressed per hectare of pond area because bullfrogs remain close to the pond after metamorphosis.

‡ Capture–mark–recapture study period, years.

§ Number of frogs recaptured at least once after the first marking occasion.

al. 1999), necessitating the development of effective bullfrog control programs (Banks et al. 2000). Current control efforts range from removal of breeding adults alone to removal of all life stages. The efficacy of these efforts, in relation to reduction in population growth or cost-effectiveness, has not been evaluated. In this paper, using bullfrog control as an example, we illustrate how demographic modeling can be used to design and assess effectiveness of control of invasive organisms with complex life cycles.

There are few previous data on the demography of introduced bullfrog populations but, in general, amphibian population growth rate is more sensitive to changes in postmetamorphic survival rates than to changes in fecundity or tadpole survival (Lampo and De Leo 1998, Biek et al. 2002, Vonesh and De la Cruz 2002). Therefore, we first estimated the postmetamorphic survival of bullfrogs using capture–mark–recapture (CMR) methods and assessed the spatial and temporal variation in these survival rates.

We then constructed a stage-based population projection matrix, using the CMR estimates of postmetamorphic survival, field estimates of fecundity and tadpole transformation rates, and estimates of tadpole survival rates from the published literature. Using sensitivity and elasticity analyses, we identified life stages and vital rates that strongly influenced population growth rate. Targeting these is considered the most effective way to control populations (Caswell 2000, De Kroon et al. 2000, but see Heppell et al. 2000). We then discuss the effort required to implement these control strategies, and their effect on population growth rate and other vital rates.

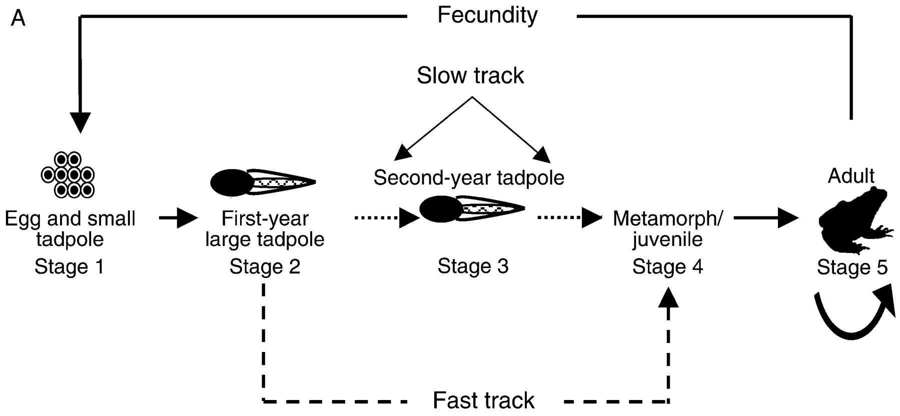
METHODS

Field sites and marking

The four study ponds are in suburban Victoria, British Colombia, Canada (48°39′ N 123°25′ W) (Table 1). Beaver and Copley Pond are close together (250 m) near the putative historic point of introduction of bullfrogs, while Trevlac Pond is 4 km away and Prior Lake 6.5 km away from the first two ponds. Bullfrog populations have been documented in the Beaver Pond area in the center of the range since the 1960s. The populations at Trevlac Pond and Prior Lake are part of a recent bullfrog range expansion in the 1990s. All four sites are permanent ponds with densely vegetated shorelines of cattails (*Typha latifolia*), hardhack (*Spiraea douglasii*), and willow (*Salix* sp.). Although there were a number of bullfrog ponds in the vicinity of each of the four study ponds and bullfrogs may have migrated among these ponds, the four sites were treated as separate populations because with one exception, frogs marked at one study pond were not found at another study pond. One adult male marked in Copley Pond was recaptured the following year at Beaver Pond 250 m away.

The bullfrog life cycle in our study region was deduced from field observations and mark–recapture studies (Govindarajulu 2004). The bullfrog life cycle consisted of yearly transitions through the following stages: egg/small tadpole, first-year tadpole, second-year tadpole, metamorph/juvenile, and adult (Fig. 1). There were two alternate pathways to metamorphosis, the ‘‘fast track’’ where tadpoles metamorphosed at the end of one year and the ‘‘slow track’’ where tadpoles metamorphosed at the end of two years. Bullfrogs reached adult size (>150 g) two years after metamorphosis, and started reproducing in their third year after metamorphosis. Unlike many amphibians that move into upland habitats during the postmetamorphic phase, bullfrogs feed, mate, and hibernate in permanent ponds (Bruneau and Magnin 1980*a*, Bury and Whelan 1986). This enabled us to use pond characteristics to examine factors affecting spatial variation in postmetamorphic survival rates.

For the capture–mark–recapture studies (CMR), bullfrogs were captured by hand at night from a canoe between the months of May and October (Table 1). The frogs were taken to the laboratory where they were measured and individually marked using an inert elastomer paint injection (Northwest Marine Technologies, Inc., Shaw Island, Washington, USA) between the two layers of webbing membranes in their hind feet. We used a numeric code by using multiple marks in various web positions. We observed that all the marks were



B

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & 0 & 0 & 2080 \\ 0.070 & 0 & 0 & 0 & 0 \\ 0 & 0.078 & 0 & 0 & 0 \\ 0 & 0.016 & 0.020 & 0 & 0 \\ 0 & 0 & 0 & 0.129 & 0.318 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{pmatrix}_{t}$$

FIG. 1. (A) Bullfrog life cycle graph showing alternate pathways: slow track (dotted lines), where tadpoles attain metamorphosis after two years; fast track (dashed line), where tadpoles attain metamorphosis in one year; and adult self-loop (bold). (B) The corresponding bullfrog population projection matrix. The subdiagonal elements represent growth, the diagonal elements represent stasis, and the top row indicates fecundity. The two vectors are the number of individuals in each stage at times $t + 1$ and t.

clearly retained by frogs that were captured repeatedly over many years, suggesting that mark loss was negligible. The frogs were returned to the ponds the afternoon following capture. There was a minimum of three capture occasions each year at each site, except for 2003 when there was only one recapture occasion.

Survival rate estimation using capture–mark–recapture (CMR) modeling

Analyses followed protocols set out in Lebreton et al. (1992) and survival and recapture probabilities were estimated using maximum-likelihood methods implemented in the program MARK (White and Burnham 1999). The CMR modeling method accounts for the fact that not all marked living individuals are recaptured at every sampling occasion and separates survival probability from recapture probability, where recapture refers to the probability of capturing an individual given that it is alive and in the study area on that occasion (Lebreton et al. 1992). This method cannot distinguish permanent emigration from mortality.

Factors thought to affect survival and recapture rates were used to frame a set of hypotheses, which were expressed as an a priori set of alternate models (Anderson et al. 2000). We examined variation in yearly survival between ponds over the four years for which data from all ponds were available (1999–2002). Recapture probability was modeled as dependent on pond, year, pond area, and capture effort. Yearly survival probability was modeled as varying among ponds, among years, and depending on the interaction between ponds and years. The interaction term examines whether the survival rates vary asynchronously among the ponds. We also tested whether variation among ponds could be explained by differences in the population density and/or mean size of frogs in each pond. Metamorphs were excluded from this analysis due to sparse data in Copley Pond and Trevlac Pond.

Information-theoretic methods were used to estimate the formal likelihood of each model given the data and rank support for each model (Anderson et al. 2000). Model selection was based on the sample size adjusted Akaike's Information Criterion ($\mathrm{AIC_c}$) (Burnham and Anderson 2002). $\mathrm{AIC_c}$ mediates the trade off between deviance explained and the number of parameters used, and simulations have shown that this method is better at recovering the true underlying model compared to likelihood ratio tests (Burnham et al. 1995). The model with the lowest $\mathrm{AIC_c}$ value is the model best supported by the data. Akaike weights indicate the support from the data for a particular model relative to the other models in the set, and sum up to 1 across all models. The ratios between the Akaike weights of two models give their relative support (e.g., a model with Akaike weight of 0.5 is twice as well supported as a model with Akaike weight of 0.25).

The assumption of CMR analysis of homogeneous survival and recapture among individuals within a recapture interval was confirmed for each pond by testing the time-dependent Cormack-Jolly-Seber (CJS) model using program RELEASE implemented within program MARK (Burnham et al. 1987).

TABLE 2. Calculation of transition probabilities.

Transition	a_{ij}†	Parameter estimation equation
Egg to tadpole survival	a_{21}	$\phi_{\text{emb}} \times \phi_{\text{v. s. tad}} \times \phi_{\text{s. tad}} \times \phi_{\text{s. tad overw}} \times \phi_{\text{l. tad}}$ $0.92 \times 0.40 \times 0.87 \times 0.23 \times 0.95 = 0.0704$
Slow track, tadpole to tadpole	a_{32}	$\phi_{\text{l. tad}} \times \phi_{\text{l. tad overw}} \times \phi_{\text{l. tad}} \times \sigma_{\text{late}}$ $0.97 \times 0.26 \times 0.95 \times 0.325 = 0.0775$
Slow track, tadpole to juvenile	a_{43}	$\phi_{\text{met}} \times \phi_{\text{met overw}} \times \phi_{\text{juv}}$ $0.380 \times 0.097 \times 0.531 = 0.0196$
Fast track, tadpole to juvenile	a_{42}	$\phi_{\text{l. tad}} \times \phi_{\text{met}} \times \phi_{\text{met overw}} \times \phi_{\text{met}} \times \phi_{\text{juv}} \times \sigma_{\text{early}}$ $0.98 \times 0.62 \times 0.097 \times 0.62 \times 0.66 \times 0.68 = 0.0160$
Juvenile to adult	a_{54}	ϕ_{juv} 0.13
Adult survival	a_{55}	ϕ_{ad} 0.32
Fecundity	a_{15}	$\phi_{\text{ad}} \times \text{sex ratio} \times \text{clutch size}$ $0.32 \times 0.5 \times 13\,014 = 2082$

Notes: Symbols are ϕ, survival rate (subscript indicates life stage); σ_{early} or σ_{late}, early or late metamorphosis. Estimated vital rates are mean ± SE unless otherwise indicated. Embryo survival was 0.92 ± 0.05 (SD) (Biek et al. 2002). We assumed that, for the first two weeks after hatching, bullfrog tadpoles <1 cm ($\phi_{\text{v. s. tad}}$) would have survival rates similar to similarly sized *Hyla regilla* tadpoles in our region, for which we had precise survival estimates (0.402 + 0.03; Govindarajulu 2004). We assumed that bullfrog tadpoles were small (<5 cm total length) until they emerged from their first hibernation. Small tadpole and large tadpole survival over the summer ($\phi_{\text{s. tad}}$, 0.87 ± 0.07 and $\phi_{\text{l. tad}}$, 0.95 ± 0.05) and the winter ($\phi_{\text{s. tad overw}}$ 0.23 ± 0.06 and $\phi_{\text{l. tad overw}}$, 0.26 ± 0.09) were estimated from the literature (Cecil and Just 1979, Werner 1994). Fast-track tadpoles metamorphosed by August of the second year, and slow-track tadpoles metamorphosed in July of the third year. We estimated the probability of early or late metamorphosis ($\sigma_{\text{early}}/\sigma_{\text{late}}$) by sampling tadpoles in ponds in May (Beaver Pond fast track, 60%; Trevlac Pond fast track, 75%). Survival rates of the terrestrial stages were mean CMR (capture–mark–recapture) survival rates from the four ponds. For this analysis, we used three postmetamorphic size classes: metamorphs, juveniles, and adults. Bullfrogs entered the first winter as metamorphs approximately one month (fast track) or two months (slow track) after transformation. We estimated daily survival rate of metamorphs during the active season as 0.984 ± 0.004 (60 d) and during the winter as 0.989 ± 0.003 (210 d). We considered them to be juveniles when they were >30 g, ~60 active days post-transformation. Egg masses contained an average of 13 014 ± 7296 eggs (mean ± SD, $N = 15$).

† The probability of changing from stage j to stage i in one time step.

Matrix population modeling

We modeled population dynamics using a stage-based, linear, time-invariant, matrix model with a one-year projection interval (Fig. 1). In this study, we estimated fecundity, tadpole transformation probability, and growth and survival of postmetamorphic stages. Tadpole and embryo survival rates were taken from the literature. Each matrix element represents transition over the course of a year and is composed of a number of growth and survival probabilities because bullfrogs develop through multiple distinct phases during each time step (see Table 2 for information on how the matrix elements were composed and for the parameter estimates). These growth and survival probabilities are called lower level vital rates (Caswell 2001). The goal of the population modeling was to explore how the population growth rate would be affected by changes to lower level vital rates brought about by control efforts (Caswell 2000, 2001).

Following Caswell (2001), we estimated the asymptotic population growth rate λ as the dominant eigenvalue of the projection matrix, and the sensitivity of λ to small additive changes in each matrix element and lower level vital rate. While the sensitivity analysis measures the impact of absolute changes (e.g., removing a specified number of individuals, or, more precisely, reducing survival/reproduction by a specified absolute amount) in matrix elements on λ, these estimates may not readily be comparable if the elements are measured on different scales (e.g., survival rates and clutch size). Therefore, we also estimated the proportional effects (e.g., removing a specified proportion of individuals) of variation in matrix elements on λ using elasticity analyses (Caswell 2001).

Bullfrogs are unusual among anurans in having two alternate life-history pathways to metamorphosis, in addition to adults surviving multiple years to contribute to overall population growth (Fig. 1). The elasticities to changes in matrix elements along a particular pathway are equal as long as the matrix elements only contribute to a single pathway (or the same set of pathways). For example, removing 50% of the tadpoles has the same effect as removing 50% of the juveniles (which would, of course, involve removing more individual tadpoles because tadpole densities are higher). We, therefore, used loop analysis, which is an extension of elasticity analysis, to compare the relative contribution of these alternate life-history paths to overall population growth rate (Van Groenendael et al. 1994, De Kroon et al. 2000, Heppell et al. 2000). As for the elasticities of the individual elements, the sum of all loop elasticities is equal to 1 (Van Groenendael et al. 1994, Wardle 1998).

Strictly speaking, inference from sensitivity and elasticity analyses applies only to very small changes around the transition elements, because of potential non-linearity in the relationship between the transition elements and λ (De Kroon et al. 2000). To visualize

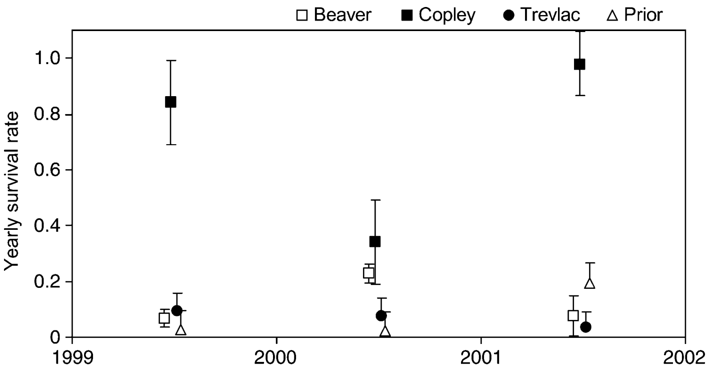


FIG. 2. Yearly survival rate of postmetamorphic bullfrogs (>30 g in size) in the four study ponds estimated using top model ϕ(pond × year)p(.). Yearly survival rates varied asynchronously among ponds. The error bars are 95% CI.

large changes that can result from control efforts, we ran a numerical simulation and plotted λ against various proportions of tadpoles entering the fast-track transition. We repeated the simulation assuming metamorph survival was decreased by one-half and one-fourth or increased by two and four times of its current value through control efforts (Fig. 3). Metamorph survival rates can increase when control efforts target adult bullfrogs thereby decreasing cannibalism on metamorphs.

The confidence intervals for the asymptotic population growth rate and the sensitivities of the lower level vital rates were calculated empirically using bootstrap methods. First, we generated 10 000 transition matrices in which the elements were calculated by randomly drawing values from a normal distribution with mean and variance equal to the logit transformed estimate of the lower level vital rates. For each of these transition matrices, sensitivity and elasticity analyses were performed as above, and population growth rate λ calculated. After sorting these values by magnitude, the 250 and 9750 bootstrap replicates represent the lower and upper 95% confidence limit. Matrix analyses were performed using R (R Development Core Team 2003) and S-plus-2000 software packages (Insightful Corporation, Seattle, Washington, USA).

RESULTS

Postmetamorphic survival rates: variation among ponds

Postmetamorphic survival rates varied among ponds and among years (Fig. 2). Overall, Copley Pond had the highest survival rates in all years (Fig. 2). Survival rates in the other three ponds were similar and much lower than that in Copley Pond. The only models that had substantial support from the data retained the interaction term between year and pond (Model 1 and Model 2 in Table 3). The retention of the interaction term in the top models shows that the temporal variation in survival rates among ponds was asynchronous. Among-pond variation was not explained by the differences in mean adult frog size (Models 3 to 5 in Table 3) or bullfrog population density differences among ponds and years (Models 7 and 10 in Table 3).

TABLE 3. The 10 best models for survival and recapture rates of bullfrogs in the four ponds (ϕ, survival rate; p, recapture rate).

No.	Model	AIC_c	ΔAIC_c	Akaike weight	K	Deviance
1	ϕ(pond × year) p(.)	278.96	0.00	0.55	13	12.33
2	ϕ(pond × year) p(effort)	279.42	0.46	0.44	14	10.66
3	ϕ(size + size^2) p(.)	289.67	10.71	0.00	4	41.77
4	ϕ(pond + size + size^2) p(.)	291.23	12.27	0.00	7	37.17
5	ϕ(size + size^2) p(effort)	291.60	12.64	0.00	5	41.66
6	ϕ(pond) p(.)	291.61	12.65	0.00	5	41.67
7	ϕ(pond + density) p(.)	292.82	13.86	0.00	6	40.83
8	ϕ(pond) p(effort)	293.58	14.62	0.00	6	41.58
9	ϕ(pond + year) p(.)	294.36	15.39	0.00	7	40.30
10	ϕ(pond + density) p(effort)	294.73	15.77	0.00	7	40.67

Notes: Factors included in the models are shown in parentheses. ‘‘Size’’ refers to the mean size of adult bullfrogs in each pond, ‘‘effort’’ is the number of capture occasions in a given year, ‘‘.’’ indicates that the probability was held constant, ‘‘×’’ indicates the inclusion of interaction terms (main effects + interaction terms); ‘‘+’’ indicates additive model (main effects alone). Akaike’s Information Criterion adjusted for sample size (AIC_c) assesses the parsimony of the model. Models are arranged in descending order of parsimony. ΔAIC_c is the difference between a given model and the best model. Akaike weights show relative support for a particular model. K denotes the number of parameters included in the model. Deviance is the difference in the log-likelihood between the current model and the saturated model, where the saturated model is the one where the number of parameters equals sample size.

TABLE 4. Sensitivity and elasticity values of bullfrog population growth rate to variation in matrix elements (see Fig. 1).

Transition	Element a_{ij}	Sensitivity (s_{ij})	Elasticity (e_{ij})
Egg to tadpole survival	a_{21}	2.59	0.213
Slow track, tadpole to tadpole	a_{32}	0.23	0.021
Slow track, tadpole to juvenile	a_{43}	0.93	0.021
Fast track, tadpole to juvenile	a_{42}	10.25	0.192
Juvenile to adult	a_{54}	1.41	0.213
Adult survival	a_{55}	0.34	0.126
Fecundity	a_{15}	8.7×10^{-5}	0.213

Note: Matrix element a_{ij} quantifies the probability of changing from stage j to stage i during one time step.

Mean recapture rate per year for all ponds was 0.84 ± 0.09 (mean ± SE). The model with a constant recapture rate in all ponds and over years was as well supported (Model 1 in Table 3) as the model where recapture probability was a function of the number of capture occasions per year (Model 2 in Table 3, ratio of Akaike weights = 1.25), and the data do not allow us to clearly distinguish between these two models.

Population matrix modeling

Population growth rate.—The asymptotic population growth rate estimated from the mean transition matrix indicated a stable or slightly declining bullfrog population ($\lambda = 0.86$, bootstrap 95% CI = 0.58–1.12). At stable age distribution, the proportion of individuals in each of the five life stages was 91.58% eggs/small tadpoles, 7.54% large tadpoles, 0.68% second-year large tadpoles/metamorphs, 0.16% metamorphs/juveniles, and 0.04% adults.

Sensitivity analysis.—The sensitivity analysis showed that the population growth rate was most sensitive to changes in the fast-track tadpole transformation to juveniles (matrix element a_{42} Table 4). This transition element is a product of tadpole survival rate, probability of metamorphosis, metamorph survival, and juvenile survival (Table 2). Examining the sensitivities of the lower level vital rates clearly showed that population growth rate is most sensitive to both metamorph and juvenile survival, and less sensitive to the probability of early vs. late metamorphosis and tadpole survival (Table 5).

Elasticity and loop analysis.—Elasticity analysis showed that relative contribution to population growth rate was more or less evenly distributed amongst most individual life cycle transitions (Table 4). The exceptions to this pattern were the transition from first- to second-year tadpoles, and from second-year tadpoles to juveniles. These transitions had low elasticity values. Loop analysis showed that the number of individuals developing along the fast-track pathway was the most important determinant of population growth (loop elasticity of 0.77; bootstrap 95% CI, 0.62–0.85), compared to the adult self-loop (0.13, 95% CI, 0.08–0.24) and the slow-track development loop (0.10, 95% CI, 0.04–0.21).

Numerical simulation.—Since the sensitivity and loop analysis highlighted the importance of early vs. late transformation and early postmetamorphic survival rates, we ran numerical simulations to assess their effect on population growth rate λ. We varied probability of early vs. late transformation from 0% to 100%, and varied metamorph survival from 0.009, which is one-fourth of the current value, to 0.148, which is four times its current value. Numerical simulation showed that λ increases almost linearly with increasing proportions of fast-track tadpoles (Fig. 3). Similarly, population

TABLE 5. Sensitivity of λ to changes in lower level vital rates.

Lower level vital rate	Sensitivity (95% CI)
ϕ_{emb}	0.20 (0.12 to 0.27)
$\phi_{\text{v. s. tad}}$	0.45 (0.28 to 0.62)
$\phi_{\text{sm tad summ}}$	0.21 (0.13 to 0.28)
$\phi_{\text{sm tad win}}$	0.79 (0.44 to 1.29)
$\phi_{\text{lg tad summ}}$	0.39 (0.24 to 0.51)
$\phi_{\text{lg tad win}}$	0.068 (0.046 to 0.095)
$\sigma_{\text{early}}/\sigma_{\text{late}}$ metamorphosis	0.19 (0.08 to 0.29)
$\phi_{\text{met summ}}$	0.48 (0.28 to 0.78)
$\phi_{\text{met win}}$	1.88 (0.94 to 5.08)
ϕ_{juv}	1.70 (0.82 to 2.15)
ϕ_{ad}	0.91 (0.75 to 1.20)
Clutch size	1.4×10^{-5} (8.4×10^{-6} to 2.0×10^{-5})

Note: The elasticities of lower level vital rates are equal to the elasticity of the corresponding matrix element (Table 4), or the sum of the elasticities of all matrix elements to which a lower level vital rate contributes.

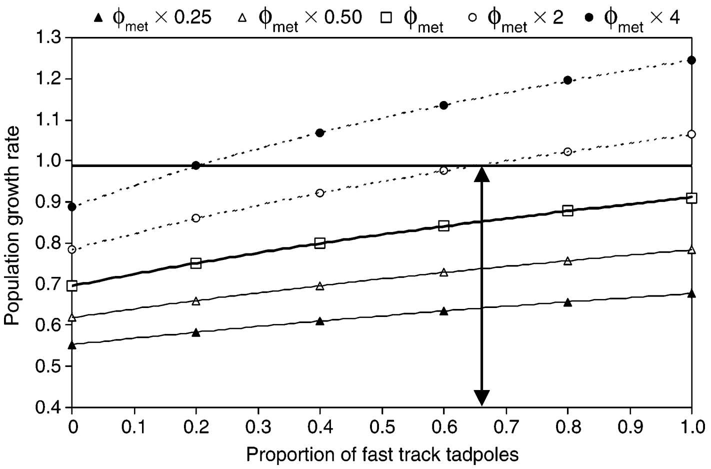


FIG. 3. Simulation of the effect that an increasing proportion of fast-track tadpoles has on projected population growth rate (open squares, bold line). The other vital rates are as estimated in the study. The two curves below the bold line indicate the same simulation but with metamorph survival rate (ϕ_{met}) reduced to one-half and one-fourth its current value (0.037), respectively, through control efforts (triangles, solid line). The two curves above the bold line indicate the same simulation, but with metamorph survival rates increased to double and quadruple its current value, respectively. Metamorph survival rates may increase due to decreased predation when adult bullfrogs are removed in control efforts (circles, dotted lines). This also accounts for the possibility that permanent emigration may have inflated our mortality estimates for metamorphs. The proportion of fast-track tadpoles observed in this study was 0.68 (double headed arrow).

growth rate increased rapidly with increasing metamorph survival rates especially at higher proportions of fast-tracking tadpoles.

DISCUSSION

The design of effective control programs of invasive species is often hampered by the lack of basic demographic information on these populations. The introduced bullfrogs in western North America are no exception. In this study, we provide basic information on the life cycle of bullfrogs and estimates of survival and growth of postmetamorphic stages. Combining this with estimates of tadpole survival rate from the literature we were able to parameterize a stage-structured population projection matrix. Perturbation analysis of this matrix enabled us to identify the proportion of early-metamorphosing tadpoles (fast-track) and early postmetamorphic survival as the vital rates with potentially large effects on population growth rate. Examining factors that affect these vital rates would be important in management strategies to control the spread of bullfrogs.

The proportion of tadpoles that can fast-track depends on their development rate, and development rate is strongly influenced by density and temperature (Harkey and Semlitsch 1988, Newman 1998). High tadpole density has clearly been shown to decrease development rates (Bruneau and Magnin 1980*b*, Werner 1994, Kupferberg 1997, Govindarajulu 2004). Temperature affects development rates both through physiological pathways and by influencing the growth of periphyton, the main food source of tadpoles (Viparina and Just 1975, Seale 1980, Harkey and Semlitsch 1988, Newman 1998, Alvarez and Nicieza 2002).

We assessed how density dependence could alter the outcome of a hypothetical tadpole control action using a numerical example that reduced tadpole survival by 50% thus resulting in a 50% decrease in tadpole density. In the absence of density dependent effects on other vital rates, decreasing tadpole survival by 50% in our model decreased λ from 0.85 to 0.74. In two separate experiments, halving densities of bullfrog tadpoles led to an average of 19% increase in development rate (Govindarajulu 2004). Halving densities in two closely related European water frog species (*Rana lessonae* and *R. esculenta*) increased their postmetamorphic survival by a factor of 1.6 (Altwegg 2002). When these density dependent effects were incorporated into the model with other vital rates unchanged, λ decreased only to 0.83. Therefore, density dependence would compensate for almost all of the effect of this hypothetical control action. These calculations assume that density dependence is equally strong across all densities and habitats. Both development and survival estimates were obtained from density manipulations conducted in artificial ponds, which may overestimate the strength of density dependence in natural ponds (Skelly and Kiesecker 2001). On the other hand, in natural ponds when *Rana temporaria* tadpole density was reduced to 25%, tadpole survival rates increased by a factor of 1.5 to 5.2 (Loman 2004). This suggests that the effect of removing tadpoles can be offset by compensatory increases in tadpole survival and other vital rates due to density dependence, and argues against the partial removal of tadpoles as part of a bullfrog control strategy.

Early postmetamorphic survival rates in bullfrogs also had a strong influence on population growth rates. This agrees with previous studies that have used matrix modeling to study frog population dynamics (Lampo and De Leo 1998, Biek et al. 2002, Vonesh and De la Cruz 2002). Postmetamorphic survival rates in bullfrogs were variable and this variation was asynchronous among the four study ponds (Fig. 2). Extreme weather events such as harsh winters and drought are thought to be related to catastrophic mortality in frogs (Howard 1981, Shirose et al. 1993, Shirose and Brooks 1995, Anholt et al. 2003). These weather events tend to synchronize survival rates at the landscape level. In the absence of such extreme weather events, we may expect pond differences in structure and surroundings, predator density, food availability, competition, and interaction among these factors to have a strong influence on the postmetamorphic survival rates causing asynchronous variation across sites (Skelly et al. 1999, Reaser 2000, Trenham et al. 2003). Of these variables we only had quantitative data on bullfrog density, which is often used as a surrogate variable for intraspecific competition.

Introduced species are expected to have high survival rates during the early colonization phase due to low intraspecific densities and paucity of predators and parasites (Fagan 2002, Mitchell and Power 2003, Torchin et al. 2003) and these rates are expected to decrease with time as intraspecific density, predators, and parasites accumulate (Lampo and De Leo 1998, Bohn et al. 2004). The population density of bullfrogs in the center of the range at Copley and Beaver Ponds was indeed higher than in the periphery in Trevlac Pond and Prior Lake (Table 1). However, the oldest populations at the center of the introduced range in Copley and Beaver Ponds had higher survival rates (Fig. 2) than the two recently colonized ponds at the periphery of the range. This, in accordance with previous studies, suggests that density-dependent competition may not be the major factor controlling postmetamorphic survival rates (Lampo and De Leo 1998).

Predation rate on bullfrogs in our region has not been quantified. However, there is good evidence that large bullfrogs are important predators on small frogs (Werner et al. 1995, Govindarajulu 2004). Almost half the large bullfrogs in our region were found to have small bullfrogs in their stomachs (Govindarajulu 2004). This suggests that metamorph survival rates during the active season may be controlled by adult bullfrog density, although we lack sufficient data to explicitly test this hypothesis. Numerical simulation shows that population growth rate increases rapidly when metamorphic survival rates are doubled or quadrupled (Fig. 3). In terms of a bullfrog control strategy, the negative effect on population growth rate achieved by removing bullfrog adults may be compensated to some degree by the positive effect of increased metamorph survival rates on population growth.

The projected asymptotic population growth rate from the matrix model suggested a stable or slightly declining population at our study ponds. However, bullfrogs in our study region have been expanding their range at the landscape level. Taken together, this suggests that there may have been significant permanent emigration of postmetamorphic stages from the study ponds. Using CMR techniques, permanent emigration cannot be distinguished from mortality. This could account for the estimates of survival in this study being lower than those published for ranids elsewhere (Willis et al. 1956, Durham and Bennett 1963, Bruneau and Magnin 1980*a*, Shirose and Brooks 1995, Biek et al. 2002, Anholt et al. 2003). Although we observed large numbers of metamorphs emigrating in the fall, our four study ponds were too far apart to be able to detect and estimate successful interpond migration rates.

Migration rates of 8% have been recorded for bullfrogs dispersing among ponds that are 150–1200 m apart (Willis et al. 1956) and can be higher for metamorphs (Shirose et al. 1993, Shirose and Brooks 1995). Metamorphic bullfrogs that emigrate from natal ponds in late fall will perish unless they find permanent ponds to overwinter (Willis et al. 1956, Shirose and Brooks 1995). If we assumed that a percentage of the metamorphs that emigrated from the study ponds survived at other ponds in the vicinity, and that an equal number of successful immigrants arrived at the study pond from these other ponds, then metamorph survival rate will be increased by the percentage of successful interpond migration. The numerical simulation showed that increasing metamorph survival causes a rapid increase in population growth rates (Fig. 3). The increasingly frequent conversion of temporary wetlands to permanent farm and ornamental ponds could therefore favor the spread of bullfrogs by increasing postmetamorphic survival rates. In this case, human habitat modification could increase a vital rate that strongly influences population dynamics of an introduced species thereby favoring its population growth and range expansion.

The cost of control of a given life stage will vary widely depending on methods used, habitat characteristics, and population density. However, population sensitivity analysis can also be used to compare the cost effectiveness of alternate control strategies. For example, if the cost of reducing tadpole survival is similar to that of reducing metamorph survival, then control of metamorphs will be the preferred option because reducing metamorph survival leads to greater declines in population growth rate, which is more sensitive to variation in metamorph survival. In our pilot projects, metamorphic bullfrogs were easier to capture during peak emergence (30 frogs$\cdot$person$^{-1}\cdot$h^{-1}) compared to juveniles and adult bullfrogs (0.5–2 frogs$\cdot$person$^{-1}\cdot$h^{-1}). Tadpole capture rates using dip nets varied from 60–150 tadpoles$\cdot$person$^{-1}\cdot$h^{-1} for small tadpoles to 10–60 tadpoles$\cdot$person$^{-1}\cdot$h^{-1} for large tadpoles, depending on habitat condition and tadpole density. Assuming a stable age distribution and given our sensitivity estimates (Table 5), removing metamorphs is the most effective strategy in our area. For every hour spent catching metamorphs, one would have to spend 3.5 h catching adults, 8 h catching juveniles, 23 h catching large tadpoles, and 160 h catching small tadpoles to achieve the same reduction in population growth rate. These estimates are not taking into account density dependence or cannibalism. These factors would further reduce the effectiveness of removing tadpoles or adults, respectively.

Summarizing from our modeling, our natural history observations, and from our pilot projects on bullfrog control, in addition to published information on frog population dynamics, we suggest that culling of metamorphs may be the most effective way of decreasing bullfrog population growth rates. In our modeling, early postmetamorphic survival rates had high sensitivity values (Table 4), which demonstrate a strong effect on population growth rates (Fig. 3; Lampo and De Leo 1998, Vonesh and De la Cruz 2002). Our modeling and other studies suggest that density-dependent competition may not play a strong role in postmetamorphic survival rates (Berven 1990, 1995, Altwegg 2003). This means that decreasing metamorph density, as part of a bullfrog control strategy, will not lead to compensatory increased survival rates at this life stage.

We used a time-invariant linear matrix model as an analytical tool to qualitatively assess the outcome of alternate control strategies, and this approach is a robust approximation to the nonlinear and stochastic real world (Caswell 2001). More detailed data would allow more sophisticated modeling, and we see a need for more empirical data especially in the following areas: the strength and shape of density dependence at various stages; the relationship between development time, metamorphic traits, and subsequent survival; and cannibalism rate by adults. Such data are rare, not only for bullfrogs, but also for other organisms with complex life cycles (but see, e.g., Altwegg and Reyer 2003).

Invasive species with complex life cycles pose special challenges to control efforts because targeting different life stages often requires different techniques and can have different effects on population growth rate. Sensitivity and elasticity analyses of population projection matrices are a useful tool to guide control strategies. Matrix models can be parameterized with minimal available data (Heppell et al. 2000) and therefore can be used even in the early stages of the invasion. Data from a species' native range or from related species with similar life history could be used to refine these models. In bullfrogs, as in most invasive species, the usefulness of population models in predicting outcomes and assessing cost-effectiveness of control strategies is limited by the lack of detailed demographic information, which constrains the development of realistic models. We suggest that the collection of such basic demographic information be built into the design of control programs as part of an adaptive management strategy for invasive species. We conclude that even simplified matrix models are useful in assessing alternate strategies for control and guiding research in further refining invasive species demographic modeling.

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