Animal Conservation

Animal Conservation. Print ISSN 1367-9430

Targeting eradication of introduced watersnakes using integral projection models

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Keywords
invasive species; species eradication; population ecology; management; demography; *Nerodia sipedon*; fecundity; integral projection models.

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Editor: Res Altwegg
Associate Editor: Benedikt Schmidt

Received 17 December 2017; accepted 18 March 2020

doi:10.1111/acv.12590

Abstract

Projection models are frequently used to identify and evaluate management actions to control or eradicate non-native species. Integral projection models (IPMs) are an appealing option for many taxa because IPMs can model vital rates as a function of continuous variables, like size, without discretizing into a few classes. Despite their strengths, IPMs have yet to see widespread use in invasive species management. Here, we used an IPM to evaluate management actions for an introduced population of common watersnakes (*Nerodia sipedon*) recently established in California, USA, where they pose a threat to many highly imperiled native fauna. We developed the IPM using data on the survival, growth and fecundity of native and non-native populations of *N. sipedon* to identify management targets that would facilitate its eradication. Population growth of *N. sipedon* was most sensitive to the growth and survival of snakes during their first year, when they grow from approximately 180 mm snout–vent length (SVL) to 350 mm, providing a clear target for eradication efforts. The IPM also provided finer resolution life-history information for targeting eradication than a simple size class-based matrix model. Simulated eradication effort showed funnel trapping, which targets all but the smallest and largest snakes, was more effective at decreasing population growth than hand capture focused on snakes >400 mm SVL. Our study highlights the value of IPMs for targeting eradication of introduced or invasive species, and we argue for wider adoption of these models for evaluating management actions.

Introduction

Preventing biodiversity loss often necessitates managing invasive species, a prospect made more feasible when eradication or control methods are cost-effective, given limited resources. Management efforts can be more effective when they are informed by knowledge of the species' population biology (Sakai *et al*., 2001). Matrix population models, for example, are frequently used to target control efforts for invasive species (Shea & Kelly, 1998; Govindarajulu, Altwegg & Anholt, 2005; Jiao *et al*., 2009). However, matrix models may not be ideal for species that are difficult to classify into discrete age or stage-classes, or for species whose vital rates depend on continuous characters (Easterling, Ellner & Dixon, 2000; Merow *et al*., 2014); a more suitable alternative may instead be the integral projection model (IPM). The IPM is a flexible approach that can model vital rates such as growth, survival and fecundity as a function of continuous individual state variables like length or mass (Easterling *et al*., 2000). Since their development, IPMs have been used to address a number of conservation challenges, including modeling the spread of invasive plant species (Jongejans *et al*., 2011), the effect of harvesting on animal populations (Wallace, Leslie & Coulson, 2013), and how environmental variation affects population growth in an endangered plant (Nicolè *et al*., 2011). IPMs may be especially useful for modeling the demography of endangered or recently established non-native species because they perform better than matrix models when created from small datasets (Ramula, Rees & Buckley, 2009). Despite their strengths, IPMs have yet to see widespread adoption in the study of many vertebrates or in the design of invasive species management plans.

IPMs are especially well-suited to modeling the demography of reptiles and other ectotherms. Vital rates, including fecundity and survivorship, often depend on size in ectotherms (Duarte & Alcaraz, 1989; Shine & Charnov, 1992; Shine, 2005), and are easily modeled in an IPM. Growth rates in ectotherms vary greatly among individuals and are affected by extrinsic factors like temperature or food availability (Sinervo & Adolph, 1989; Pauly, 1990; Madsen & Shine, 1993). IPMs naturally incorporate variance in individual growth trajectories from empirical data (Easterling *et al*., 2000), and can model environmental stochasticity as well (Rees & Ellner, 2009). Familiar matrix model outputs such as the asymptotic population growth rate (λ) and the

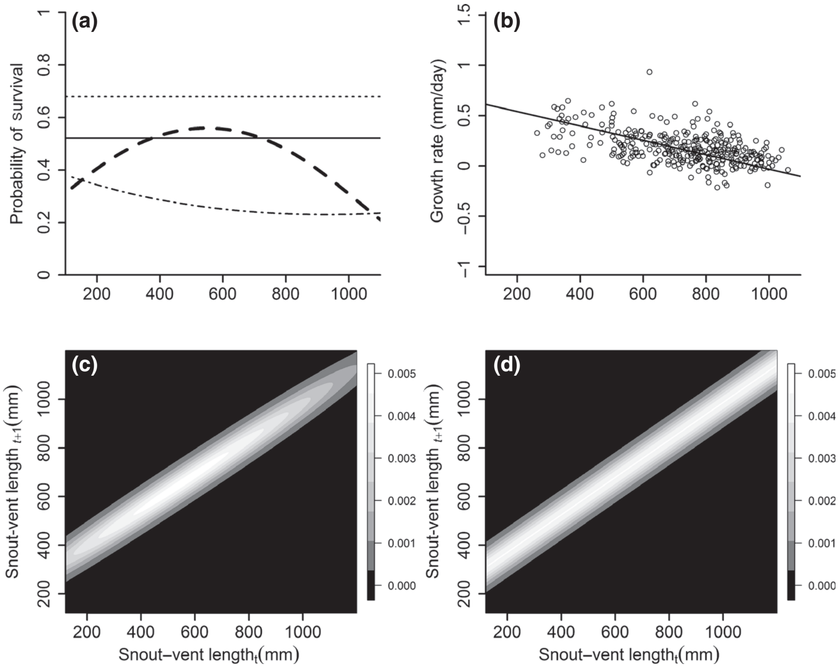

Figure 1 Survival and growth functions for integrated population models (IPMs) of *Nerodia sipedon* in its native and non-native range. (a) Four survival scenarios based on data from native and non-native populations. The dashed line represents size-dependent survival based on data from Brown & Weatherhead (1999b), the solid horizontal line represents an stable (λ = 1) 'Average' population, the dotted horizontal line represents average survival estimates from King *et al*. (2018), and the alternating dashed-dotted line represents size-dependent survival from Rose & Todd (2017). (b) Empirical data showing growth rate versus female snout-to-vent length (SVL) from native and non-native populations of *N. sipedon*. (c) The combined survival-growth component of the IPM kernel based on size-dependent survival reported from a native population by Brown & Weatherhead (1999b). (d) The combined survival–growth contribution to the IPM kernel based on size-independent survival for a stable 'Average' population. White indicates high probability of transition from the size on the x-axis at time t to the size on the y-axis at time $t + 1$, black indicates a low probability of transition. The legends in panels c and d relate the degree of shading to the probability of the size transitions in the survival–growth kernels.

sensitivity and elasticity of λ to changes in vital rates can be calculated from IPMs (Easterling *et al*., 2000; Caswell, 2001). Reptiles in particular are well-suited to IPMs because they are difficult to accurately age and because individuals are not easily classified into discrete life-stages based on size (Halliday & Verrell, 1988). Although one can create size class-based matrix models, the inferences from such matrix models are influenced by subjective decisions about the number and width of classes in the model (Enright, Franco & Silvertown, 1995; Salguero-Gómez & Plotkin, 2010). These features highlight the potential effectiveness of IPMs for modeling the demography of both endangered and invasive reptiles.

Watersnakes of the genus *Nerodia* have established multiple non-native populations in California, USA since 1992 (Balfour *et al*., 2007a, 2007b; Reed *et al*., 2016), and provide an opportunity to use IPMs to target eradication effort in an incipient invasion. Eradication of watersnakes before they become widespread is desirable given concerns about impacts to native species (Rose & Todd, 2014). Several amphibians and freshwater fish that can serve as prey for watersnakes have already declined in California and are under continued threat from non-native species (Fisher & Shaffer, 1996; Moyle, Katz & Quiñones, 2011). Also at risk are likely watersnake competitors like the federally threatened giant gartersnake (*Thamnophis gigas*) and the endangered San Francisco gartersnake (*T. sirtalis tetrataenia*), both of which have similar diet and habitat preferences to introduced watersnakes (Rossman, Ford & Seigel, 1996; Gibbons & Dorcas, 2004). Wildlife managers in California thus need to develop management plans rapidly to prevent the further growth and spread of a potentially damaging invader.

Here, we use data from both native and non-native populations of the common watersnake (*Nerodia sipedon*) to create IPMs that model the demography of this incipient invader in its native and non-native range and in growing, stable and declining populations. We use elasticity analysis to address two questions. (1) Which individuals and vital rates contribute most to population growth and should therefore be targeted with management efforts? (2) How do the inferences from a continuous IPM differ from a size class-based matrix model? We built IPMs representing declining, stable and growing populations to evaluate if conclusions from the elasticity analysis depended on the growth rate of the modeled population. Finally, we evaluate how effective trapping is likely to be as an eradication method given the size selectivity of aquatic funnel traps.

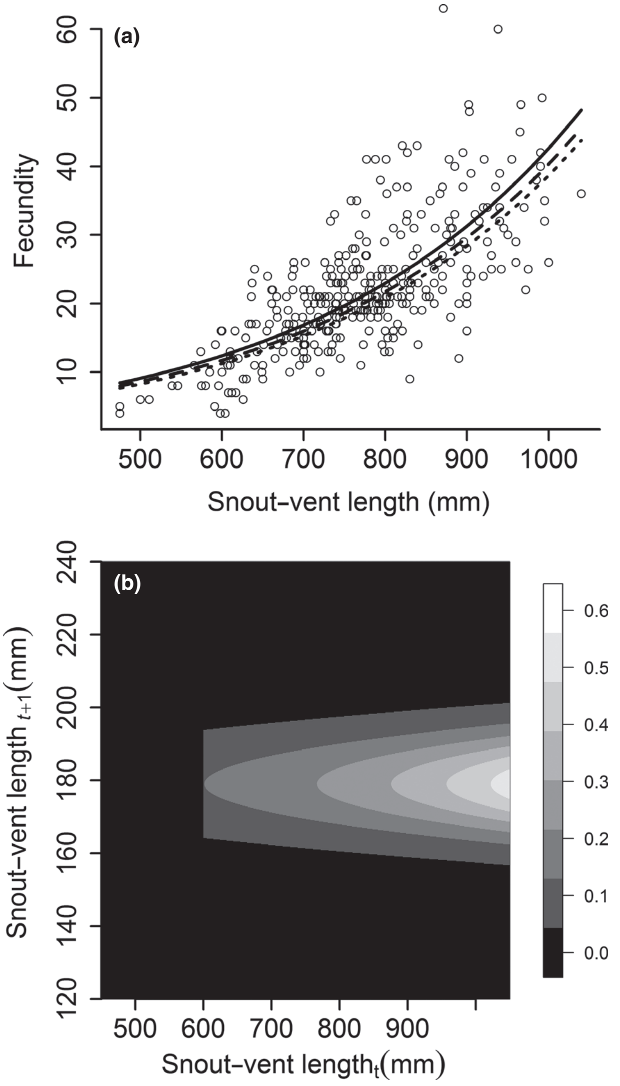

Figure 2 Female snout–vent length (SVL) and fecundity for *Nerodia sipedon*: (a) Empirical data on fecundity versus female SVL from native and non-native populations of *N. sipedon*. Lines represent mean predicted fecundity from models based on an Average population (solid line), an Ontario, Canada population (dashed line), or a Lake Erie population (dotted line). (b) The fecundity component of the Average IPM kernel with a size threshold for sexual maturity of 600 mm SVL. White indicates high probability of transition from size *x* at time *t* to size *y* at time *t* + 1, black indicates a low probability of transition.

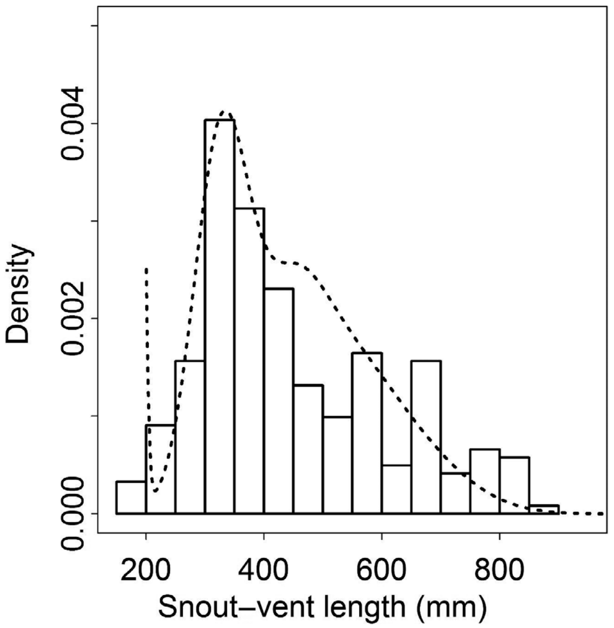

Figure 3 Comparison of predicted stable size distribution from the IPM to observed sizes in the non-native *N. sipedon* population in Roseville, California. The y-axis is truncated to highlight the distribution of females in the 'trappable' size range, ≥200 mm snout–vent length. The size–frequency histogram represents female snakes captured in the Roseville, California population of *N. sipedon* from 2011 to 2015.

Materials and methods

Integral projection models

The IPM (Eq. 1) calculates $n(z', t + 1)$, the size distribution of the population at time $t + 1$ from $n(z, t)$, the size distribution at time t multiplied by the projection kernel $K(z', z)$, integrated over Ω, the range of all possible sizes, where z is size at time t and z' is size at time $t + 1$ (Easterling *et al.*, 2000; Ellner, Childs & Rees, 2016). The kernel, $K(z', z)$, represents the probability of all possible transitions from size z at time t to size z' at time $t + 1$.

$$n(z', t+1) = \int_{\Omega} K(z', z) n(z, t) \tag{1}$$

and is composed of three vital rate functions: survival, $s(z)$, growth, $G(z'$ and fecundity, $F(z'$ (Eq. 2).

$$K(z', z) = s(z) \times G(z', z) + F(z', z) \tag{2}$$

In general, our IPM for *N. sipedon* followed the structure for a deterministic IPM outlined by Ellner *et al.* (2016). The *N. sipedon* IPM represents a post-reproductive census, where sampling takes place immediately after reproduction, to match the timing of earlier studies of the non-native population of *N. sipedon* (Figure S1). Because this is a post-reproductive model, mortality occurs before reproduction. Therefore, reproductively mature females present in year t have to survive to year $t + 1$ before they can reproduce, and the survival function, $s(z)$, is in the fecundity kernel (Eq. 3), where $f(z)$ is a function for the number of offspring produced by a female of size z, p_g (z) is a function determining whether a female is gravid or not based on its size, p_f is the proportion of offspring that are female (0.5), and $C_0(z$ is the size distribution of neonates entering the population.

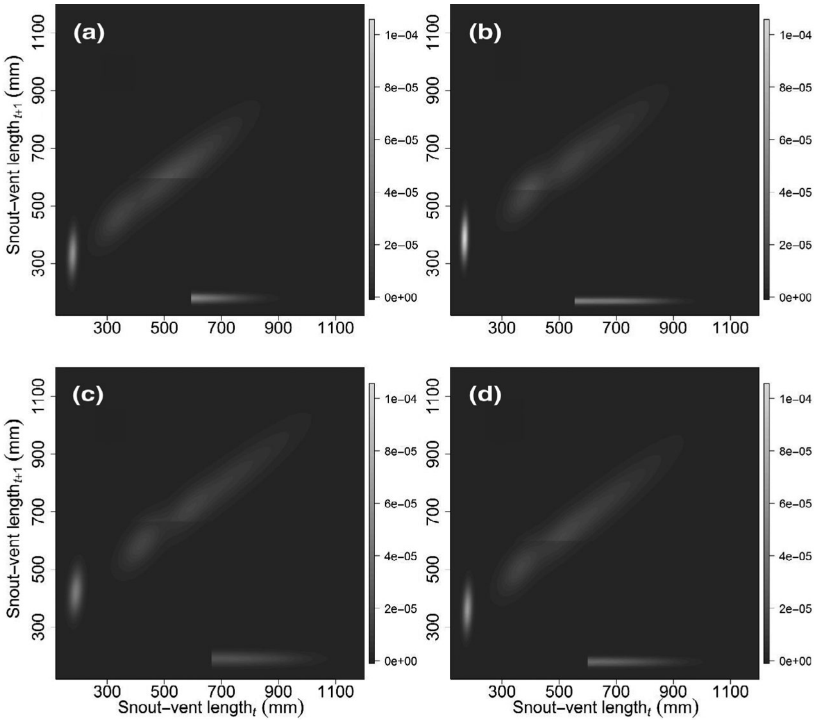

Figure 4 Elasticity of the population growth rate, λ, to changes in transition rates in the IPM kernel for four modeled *Nerodia sipedon* populations: (a) Roseville, California; (b) Ontario, Canada; (c) western Lake Erie; (d) a population with average vital rates. White indicates that perturbing the transition probability has a proportionally large effect on λ, black indicates that perturbing the transition probability has a proportionally small effect on λ. The legend relates the degree of shading to the values of the elasticity of λ to changes in transition rates.

$$F(z',z) = f(z) \times p_{\mathrm{g}}(z) \times s(z) \times p_{\mathrm{f}} \times C_0(z') \qquad (3)$$

For more details on the structure of the survival, growth and fecundity functions, see Supporting Information Appendix S1.

We constructed four IPMs representing *N. sipedon* populations in California, USA, Ontario, Canada, western Lake Erie, USA and a population with average vital rates based on all published studies of *N. sipedon* (hereinafter the ‘Average’ IPM). The size limits of the IPM were set to 120 mm snout–vent length (SVL) and 1200 mm SVL respectively to encompass the range of snake sizes in natural populations and to avoid ‘eviction’ of individuals from the model (i.e. growth beyond the size limits of the model); there was no evidence that eviction affected model results (Supporting Information Appendix S1).

We collected data on survival, growth and fecundity from published studies on *N. sipedon* in its native range. We included data from all subspecies because the origin of introduced *N. sipedon* in California is unknown. We extracted raw data from published figures using DigitizeIt software (Bormann, 2014). Data on the relationship between female SVL and fecundity came from populations of *N. sipedon* in Michigan, USA (Feaver, 1977), Missouri, USA (Bauman & Metter, 1977; Aldridge, 1982), Ohio, USA (King, Stanford & Ray, 2008), Ontario, Canada (Weatherhead *et al*., 1999) and Virginia, USA (Chin *et al*., 2013). We used a hierarchical Poisson regression to model fecundity as a function of SVL, with study as a random effect on the intercept. We used the mean estimated parameters for the size–fecundity relationship for each study population to parameterize the fecundity kernels (Appendix S1, Table S2). We parameterized growth of female *N. sipedon* using data from native populations in Michigan, USA (Feaver, 1977), western Lake Erie (*N. sipedon insularum;* King, Ray & Stanford, 2006; King *et al*., 2016) and Ontario, Canada (Brown & Weatherhead, 1999a), and a small sample of animals captured in 2 or more years (n = 17) from a non-native population in Roseville, California (Rose & Todd, 2017; Supporting Information Appendix S1). We modeled growth as a function of SVL using a hierarchical regression model with a Gaussian response. For both growth and fecundity data, we fit hierarchical regression models with a random effect of study and fixed effect of SVL on the response. We fit models in R version 3.5.1 (R Core Team, 2018), using the ‘rethinking’ package (McElreath, 2016). We ran four independent chains for 2000 sampling iterations after a warmup of 2000 iterations; all parameters showed convergence with ˆ < 1.01 (Brooks & Gelman, 1998; see Table S2 for model priors and posterior estimates). Model code is available in Supporting Information Data S1, with instructions in Appendix S2.

We used the mean estimated slope of the growth rate-size relationship, b_{g}, for the growth coefficient, k, in the von

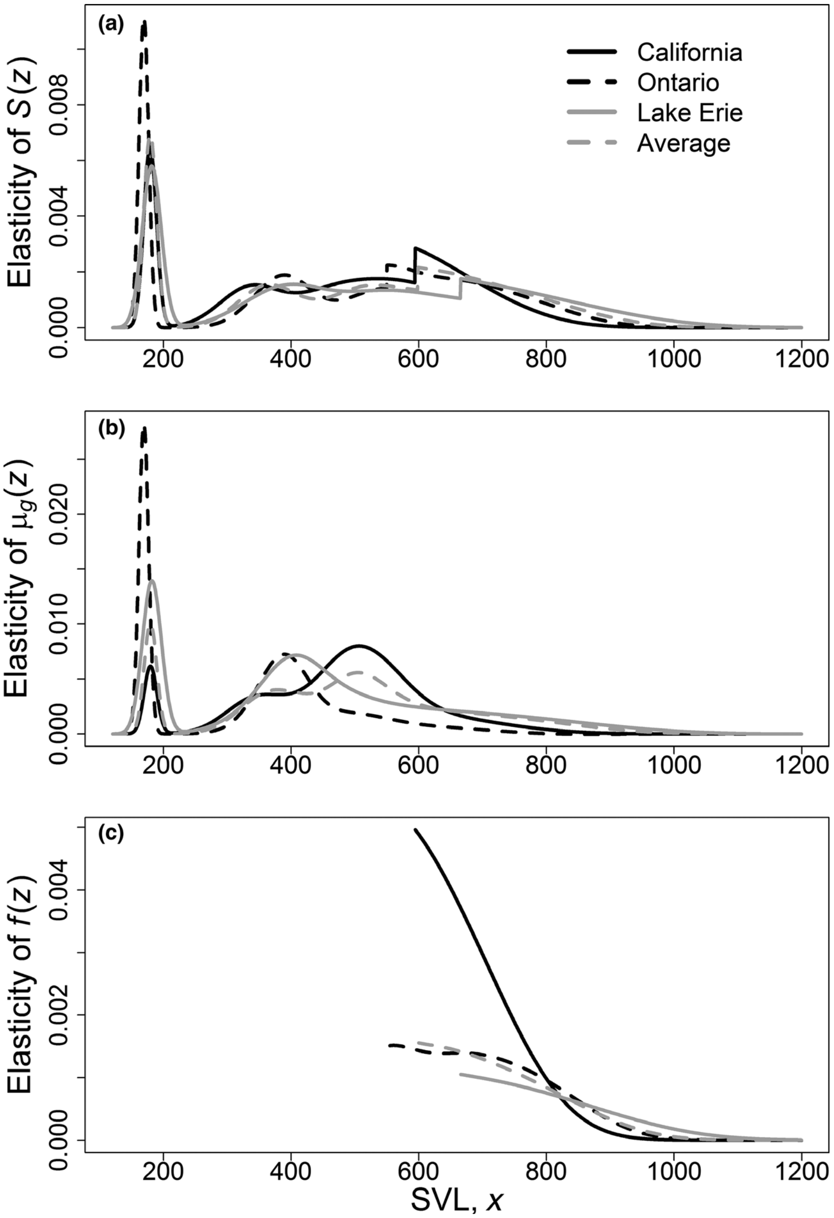

Figure 5 Elasticity of λ for three vital rate functions in the four *Nerodia sipedon* IPMs: (a) survival; (b) expected size in next year; (c) fecundity for four *N. sipedon* population models: Roseville, California (solid black line), Ontario, Canada (dashed black line) western Lake Erie (solid gray line), and a population with average vital rates (dashed gray line).

Bertalanffy growth function for the California and Average IPMs ($k = -b_g$). We used the SVL of the longest female *N. sipedon* captured in the non-native California population as the asymptotic length, L_∞, for the California IPM. For the Average IPM, L_∞ was calculated using the mean intercept (a_{g0}) and slope (b_g) parameters of the size–growth rate relationship, where $L_\infty = a_{g0}/(-b_g)$ (Supporting Information Appendix S1, Table S2). We used reported estimates of L_∞ and k from Ontario, Canada (Brown & Weatherhead, 1999a) and western Lake Erie, USA (King *et al.*, 2016) for their respective IPMs (Table 1).

Previous studies have differed in the estimated annual survival rate of *N. sipedon* and the shape of the size–survival function (Supporting Information Appendix S1). Because the sensitivity of λ to changes in vital rates can vary with the growth rate of the population (Heppell, Caswell & Crowder, 2000), the four IPMs represent four survival scenarios: (1) Quadratic size-dependent annual survival based on data from Ontario, Canada (Brown & Weatherhead, 1999b), (2) size-dependent survival estimated from the non-native population in Roseville, California from 2014–2015 (Rose & Todd, 2017), (3) average size-independent survival (0.68) from 14

Table 1 Vital rate functions used to create the Integral Projection Model and parameter estimates for each IPM

			Study population			
Demographic process	Model	Parameter	California	Ontario	Lake Erie	Average
Probability of survival	$s(z) = \text{logit}^{-1}\ (\alpha_s + \beta_{s1} \times z + \beta_{s2} \times z^2)$	α_s	−0.30	−1.30	0.75	0.09
		β_{s1}	−1.95E-03	5.62E-03	0	0
		β_{s2}	1.05E-06	−5.13E-06	0	0
Fecundity	$f(z) = \exp\ (\alpha_f + \beta_f \times z)$	α_f	0.66	0.61	0.57	0.66
		β_f	3.09E-03	3.09E-03	3.09E-03	3.09E-03
Size at maturity (mm)	$p_g = \begin{cases} 0, & if\ z < z_m \\ 1, & \text{otherwise} \end{cases}$	z_m	594	554	665	600
Proportion of female offspring	p_f	p_f	0.5	0.5	0.5	0.5
Neonate size at birth (mm)	$C_0(z') = N(\mu_{nn}, \sigma_{nn})$	μ_{nn}	179	169	190	179
		σ_{nn}	10	7.6	12.4	10
Individual growth	$G(z', z) = N(\mu_g, \sigma_g)$	L_∞	827	929	1015	941
Expected size	$\mu_g = z + (L_\infty - z) \times (1 - \exp\ (-k \times t_g))$	K	7.15E-04	0.0020	0.0017	7.15E-04
		σ_g	45.78	45.78	45.78	45.78
Growth interval		t_g	365	160	185	365
Asymptotic population growth rate	$\lambda = N_{t+1}/N_t$	λ	0.48	1.03	1.39	1

populations in Lake Erie (King, Stanford & Jones, 2018) and (4) size-independent survival (0.52), that produces a stable population ($\lambda = 1$) when combined with average fecundity and growth rates in the Average IPM (Fig. 1a).

We constructed IPMs in R version 3.5.1 (R Core Team, 2018) by adapting code from Ellner *et al.* (2016). We calculated the population growth rate, λ, and the stable size distribution (Easterling *et al.*, 2000) for each IPM. To verify that an IPM accurately captured the demography of the non-native *N. sipedon* population, we compared the stable size distribution from the California IPM to observed size–frequency histograms from the non-native population. We also calculated the average age at sexual maturity for female snakes in the model using the 'IPMpack' package in R (Metcalf *et al.*, 2013), and compared it to observed ages at sexual maturity from native populations.

We used elasticity analysis to calculate the proportional effect on λ of small perturbations of transition probabilities (Supporting Information Appendix S1; Easterling *et al.*, 2000). In addition to calculating the elasticity of λ to perturbations of the IPM kernel, we also calculated the elasticity of λ to perturbations of three component vital rate functions: growth, survival and fecundity (Ellner *et al.*, 2016).

Size class-based matrix models

For comparison to the continuous size-based IPM for the non-native California population, we constructed size class-based matrix models using the same demographic data. We first constructed a 10×10 class matrix model, then created 7×7 and 5×5 matrix models from this larger matrix by collapsing the last four (six) classes into one size class representing large adults (Salguero-Gómez & Plotkin, 2010; Supporting Information Appendix S1). We created models following a post-breeding census where females reach maturity at 4 years of age based on the results of the California IPM and empirical studies of native populations (Weatherhead *et al.*, 1995; Brown & Weatherhead, 1999b; King *et al.*, 2016). For a post-breeding model with an age at maturity of 4 years old, the first size class represents neonate snakes, the second and third size classes represent juvenile and immature females, and the fourth size class and above are adult, sexually mature females. The fourth size class is reproductive because although individuals are 3 years old at time t, they will grow, reach 4 years of age, become sexually mature and reproduce before the next census at $t + 1$ (Kendall *et al.*, 2019). We based survival probabilities for each size class on the average survival for individuals within the size range of that class. We calculated λ and the elasticity of λ to changes in matrix parameters for comparison to the IPMs. The matrix model analysis was done using custom code in R (available in Supporting Information Data S1).

Trapping effects on population growth

We simulated the effect of eradication efforts on population growth by calculating the survival rate of individuals exposed to two alternative capture methods: aquatic funnel traps or hand captures. Funnel traps exhibit size selectivity on watersnakes in three ways: (1) small neonate snakes (<200 mm SVL) can escape through the mesh openings, (2) large adult snakes (>830 mm SVL) are too big to fit through the funnel and (3) within these upper and lower limits, there is a slight increase in capture probability of *N. sipedon* with increasing SVL (Rose & Todd, 2017). In contrast, Brown & Weatherhead (1999b) found no size selectivity for hand captures of *N. sipedon* once snakes had reached 2 years. We used the catchability (q) estimate from a *N. sipedon* removal experiment in California in 2011 (Rose *et al.*, 2013) to calculate harvest mortality, $F_s = q \times E$, where E is the eradication effort (Arreguín-Sanchez, 1996). Because we lack data on the catchability of *N. sipedon* from hand captures, we assume that the average value of q is equal for both eradication methods, and that hand captures and trapping differ only in size selectivity. Therefore, to simulate an eradication regime based on hand captures, we set q to a constant value for all snakes >400 mm SVL (Figure S2). To compare the two capture methods, we calculated the change in λ with increasing eradication effort using the Average IPM. We quantify trapping eradication effort in terms of trap nights (one funnel trap active for one night), which cannot be directly translated to an equivalent amount of hand capture effort; our analysis was designed to present the expected response of a population to increasing capture effort for both methods, given the different sizes likely to be captured by each.

Results

Somatic growth rates decreased as SVL increased in *N. sipedon* (Fig. 1b). The shape of the combined survival–growth function varied slightly depending on the shape of the survival curve (Fig. 1a). With size-dependent survival, the probability of individuals' transitioning to a larger size at the next time step peaked between 400 and 600 mm SVL and declined rapidly <300 and >800 mm SVL (Fig. 1c). With size-independent survival, the survival–growth function produced a Gaussian ridge with equal probability of transition along the mean growth function (Fig. 1d). Fecundity increased with female size (Fig. 2a). The size of neonates produced by reproductive females followed a Gaussian distribution with a peak transition probability at 179 mm SVL and a declining probability of producing larger or smaller offspring (Fig. 2b).

The California IPM built with the low survival rate and slow growth rate using estimates from the non-native population represents a rapidly declining population, λ = 0.48, which corresponds to drought-induced declines in abundance observed from 2013 to 2015 (Rose & Todd, 2017). To produce a stable population with λ = 1 given the mean growth and fecundity estimates in the Average IPM, annual survival must equal 0.52. The Ontario IPM had a population growth rate representing a slowly growing population (λ = 1.03), whereas the Lake Erie IPM had a high population growth rate, λ = 1.39.

The stable size distribution for the California IPM closely matches the size distributions of captures from the non-native population in California over 4 years, except for individuals <200 mm SVL (Fig. 3), which were too small to be captured in funnel traps. The mean age at which female snakes reached the size threshold for sexual maturity was 4.2 years in the California IPM, 3.2 years in the Ontario IPM, 3.8 years in the Lake Erie IPM and 4.0 years in the Average IPM.

Elasticity analysis

Despite the differences in projected population growth, elasticity patterns were qualitatively similar for the four IPMs (Fig. 4); the elasticity of λ to changes in the IPM kernel was greatest for the growth and survival of individuals during their first year of life. Specifically, λ was highly sensitive to proportional changes in the probability of surviving the first year and growing from size at birth (150–200 mm SVL) to average size at 1 year (330–410 mm SVL) (Fig. 4). Population growth rate was less influenced by the fecundity of small adult females, represented by a ridge of high elasticity in the transition from 600–800 mm SVL to neonate size (Fig. 4). For juvenile snakes, surviving and growing to SVLs less than the threshold for sexual maturity had a small effect on λ, whereas the transition to SVLs greater than the threshold for sexual maturity had a larger effect on λ (Fig. 4).

Among the underlying vital rate functions used to build the IPM, survival of neonates had the greatest proportional effect on λ, followed by survival of females just larger than the size threshold for sexual maturity (Fig. 5a). Likewise, the expected growth of neonates had the largest elasticity, followed by the expected growth of females near the size threshold for sexual maturity for three IPMs, with the growth of sub-adult females having slightly higher elasticity in the California IPM (Fig. 5b). The fecundity of small adult females had the greatest elasticity for λ, with elasticity dropping sharply for the fecundity of larger females in the IPMs that had declining survival for large adults, or more gradually in the IPMs that had size-independent survival (Fig. 5c). These elasticity patterns were generally consistent for both size-dependent and size-independent survival, and regardless of whether the modeled population was declining, stable or growing.

The matrix models produced similar estimates of λ (0.56) as the California IPM (0.48), but the elasticity patterns were markedly different. In the matrices below, the values represent the elasticity of λ to perturbations of the corresponding matrix parameter. The elasticity of λ in the 5 × 5 California matrix model with an age-at-maturity of 4 years (as predicted by the IPM) was equal for survival of all pre-reproductive life-stages, and the sum of the elasticities (fecundity + survival) for life stages 4 and 5 was similar:

$$E_{4,5} = \begin{bmatrix} 0 & 0 & 0 & 0.10 & 0.11 \\ 0.20 & 0 & 0 & 0 & 0 \\ 0 & 0.20 & 0 & 0 & 0 \\ 0 & 0 & 0.20 & 0 & 0 \\ 0 & 0 & 0 & 0.11 & 0.08 \end{bmatrix}$$

In other words, the total proportional effect on λ of perturbing the individual matrix elements (transition probabilities) for each size class was approximately the same. For the 7 x 7 and 10 x 10 matrix models, the elasticity of λ to changes in survival of pre-reproductive size classes was again constant, but the elasticity of λ to survival and fecundity declined with increasing size for reproductively mature size classes.

$$E_{4,7} = \begin{bmatrix} 0 & 0 & 0 & 0.09 & 0.05 & 0.03 & 0.03 \\ 0.20 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.20 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.20 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.11 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.05 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.03 & 0.02 \end{bmatrix}$$

$$E_{4,10}\begin{bmatrix} 0 & 0 & 0 & 0.09 & 0.05 & 0.03 & 0.01 & 0.006 & 0.003 & 0.004 \\ 0.20 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.20 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.20 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.10 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.05 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.03 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.01 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.007 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.004 & 0.003 \end{bmatrix}$$

Trapping effects on population growth

An eradication effort based on trapping, which targets snakes between 200 mm and 830 mm SVL, resulted in a larger decrease in λ compared to hand capturing snakes >400 mm SVL for low-to-moderate levels of eradication effort (Figure S3). For a stable population in the Average IPM, reducing λ by >40% would require 1,200 trap-nights of effort with aquatic funnel traps. To achieve a 40% reduction in λ by targeting snakes >400 mm SVL with hand captures would require 2.25 times as much eradication effort, assuming equal catchability between the two methods. Only at high levels of eradication effort (equivalent to >3,600 trap-nights of effort) does removal of snakes by hand capture result in lower estimates of λ than trapping. The effect of trapping on λ asymptotes at a 50% decrease in population growth for >2,000 trap-nights of effort (Figure S3).

Discussion

Our IPM integrates data from both native and non-native populations of *N. sipedon* to model the demography of this species and provide insight into the life stages and vital rates that most influence population growth. The elasticity analysis revealed that the growth rate of *N. sipedon* populations was most influenced by the growth and survival of individuals in their first year. This bodes well for the use of trapping as an eradication method for non-native populations in California, as compared to hand capture. The size class most frequently captured in aquatic funnel traps is between 300 and 400 mm SVL, which represents individuals around 1-year of age (Rose & Todd, 2017). While neonate individuals may initially evade capture due to their small size, their capture probability in funnel traps increases greatly as they grow during their first year (Rose & Todd, 2017). In contrast to trapping, 1-year-old *N. sipedon* are difficult to capture by hand (Brown & Weatherhead, 1999b). The sensitivity of population growth to somatic growth of young snakes highlights that estimating growth rates of young snakes is an important area for future research on *N. sipedon* in California given our limited data on individual growth (Rose & Todd, 2017). Comparison of model outputs to empirical data demonstrated that the IPM accurately reflects the demography of *N. sipedon*. The stable size distribution from the IPM corresponded well with empirical size distribution data from the non-native population and the IPM produced estimates of age-at-maturity (3–4 years) that match values reported in the literature for *N. sipedon*: from 2 to 3 years in Missouri (Bauman & Metter, 1977), 3 years in Michigan (Feaver, 1977) and 4 years in Ontario and Ohio (Brown & Weatherhead, 1999a; King *et al*., 2016).

The efficacy of an IPM at modeling the demography of *N. sipedon* highlights the value of this method for species with size-dependent demography, including many ectotherms. Size-dependent survival, growth and fecundity have been reported from most reptile taxa (e.g. snakes – Weatherhead *et al*., 1999; Rose *et al*., 2018a, 2018b, lizards – Zúñiga-Vega, Méndez-de la Cruz & Cuellar, 2008, turtles – Doak, Kareiva & Klepetka, 1994, crocodilians – Dunham, Dinkelacker & Miller, 2014). IPMs also have the flexibility to model the relationship between vital rates and the state variable using complex, non-linear functions (Dahlgren, García & Ehrlén, 2011; Rose *et al*., 2019). Furthermore, it is possible to incorporate both age- and size dependence into an IPM for cases in which some vital rates vary as a function of one characteristic or the other, or both (Ellner & Rees, 2006). The ability to design models that match the demography of the study species, rather than forcing continuous and sometimes complex relationships into a few discrete parameters, is a major advantage of IPMs over matrix models.

The matrix models did not provide the detailed description of the demography of *N. sipedon* illustrated by the IPMs. Like the IPMs, the matrix models showed that survival of young, pre-reproductive snakes had the greatest proportional influence on λ. However, unlike the IPMs, in the matrix models the survival of all pre-reproductive size classes had equal effects on λ. As a result, if we had only analyzed a small matrix model that binned several pre-reproductive sizes together – for example the 5 × 5 matrix model – elasticities for each size class would have been nearly equal and there would be no clear recommendations for which life stages to target for population control, and thus which capture methods to use. Consequently, the IPM identifies more specific targets for management actions that could have the greatest effect on the growth rate of an invasive population compared to a matrix model. For example, a study using a 5-stage matrix model to identify targets for the removal of invasive American Bullfrogs on Vancouver Island, Canada found nearly equal elasticity for four of seven matrix elements – essentially all of the major life-stage transitions made the same proportional contribution to λ (Govindarajulu *et al*., 2005). Small matrix models can also produce estimates of λ that are more biased and have greater variance than comparable IPMs (Ramula *et al*., 2009). Despite their undoubted contributions to conservation, the use of matrix models has shortcomings, including frequent misspecification of models (Kendall *et al*., 2019), limitations for guiding management decisions (Mills, Doak & Wisdom, 1999), difficulty defining classes in size-based models (Vandermeer, 1978; Moloney, 1986) and the sensitivity of conclusions to subjective decisions (Enright *et al*., 1995; Salguero-Gómez & Plotkin, 2010). Furthermore, the outputs from size-based IPMs can be easily connected to concrete management actions in taxa where capture methods exhibit size selectivity (e.g. fish, Millar & Fryer, 1999; reptiles, Willson, Winne & Keck, 2008; mammals, Schofield & Barker, 2011). For example, our results showed that trapping will likely result in greater population declines for non-native *N. sipedon* than hand captures, because trapping is able to capture smaller snakes. Still, the diminishing returns on decreasing λ as trapping effort increases suggests that augmenting trapping with some hand capture efforts focused on large adults could be a successful approach to eradication. Given the advantages of using an IPM and the resources available to guide model development (i.e. Merow *et al*., 2014; Ellner *et al*., 2016), this method deserves to be more widely adopted by those studying species with size-dependent demography.

When interpreting our results, it is important to remember a few assumptions inherent to our methods. We assumed that vital rates were not density dependent in the study population. The removal of *N. sipedon* through trapping could result in compensatory growth among the remaining animals due to reduced competition. Analysis of population time series has shown evidence of density-dependence in snake populations, although density dependence was not detected in the majority of species examined (Leão, Pianka & Pelegrin, 2018). Nonetheless, ignoring density dependence, especially for a rapidly growing invasive population, could lead to misguided conclusions about how populations respond to management (Benton & Grant, 1999). We also assumed populations were at equilibrium and restricted our analysis to asymptotic dynamics. For invasive populations, size or age structure might be important for predicting population dynamics, especially in response to management actions, necessitating analysis of transient dynamics (Ezard *et al*., 2010). The short generation time of *N. sipedon* could have led to faster convergence to asymptotic dynamics, as evidenced by the similarity between the stable and observed size distributions (Koons *et al*., 2005). The transient dynamics of IPMs can be analyzed using the same mathematical tools as a matrix model (Merow *et al*., 2014). Although in the future our IPM could potentially be improved by testing for and incorporating density dependence or analyzing transient dynamics, the desire for more data should not delay action to eradicate a potentially damaging invader (Simberloff, 2003).

The invasion of non-native watersnakes into California is worrisome given the history of invasive snakes elsewhere. The invasion of Guam by the brown tree snake (*Boiga irregularis*) led to dramatic declines in native birds and lizards that served as naïve prey (Rodda, Fritts & Chiszar, 1997). The recent introduction of the Burmese python (*Python bivittatus*, to the Everglades in southern Florida, USA has also been linked to declines in native species (McCleery *et al*., 2015). To prevent *N. sipedon* from becoming a damaging invasive species in California, managers should act now to eradicate the non-native population while it is localized and at low abundance. Although the non-native population declined from 2013–2015, which is reflected in the low λ value for the California IPM, this decline occurred during an exceptional drought (Rose & Todd, 2017). Before the drought, the *N. sipedon* population had reached a high density (56 snakes/ha) and abundance (>340 individuals) in 2011, just 4 years after report of its initial discovery in 2007 (Balfour *et al*., 2007b; Rose, Miano & Todd, 2013). Waiting to initiate management of invasive species allows their distribution to broaden, which increases the cost of eradication and decreases the likelihood of eradication success (Simberloff, 2003, 2009). Also, while timely initiation of trapping efforts may prove fruitful in driving nascent populations to extinction, complete eradication will likely require trapping, ideally supplemented with hand capture effort, for several years. One or a few surviving females could re-establish a population if management efforts end prematurely. Eradication and surveillance should continue even after the population appears to be extinct to prevent recovery (Simberloff, 2009). Therefore, completely eradicating this potential invader will require long-term commitment and coordination from state and federal wildlife agencies.

Our study shows how IPMs can be used to address invasive species management and better understand the demography of reptiles and other taxa with size-dependent vital rates. An IPM not only better models the size-dependent demography of our *N. sipedon* population, but also provides more detailed information for management targets than a comparable matrix model. We found that population growth of *N. sipedon* was most influenced by the growth and survival of snakes in their first year, reflecting the fast somatic growth and early maturity in this species. Management plans should focus on using trapping methods known to capture susceptible size classes, augmented with hand captures when possible, if they are to succeed in eradicating *N. sipedon* from California. Finally, we argue for wider adoption of IPMs to study reptile population biology given well-established relationships between individual size and vital rates for many species, and the variability of vital rates among individuals, populations and environments.

Acknowledgments

We thank L. Botsford and P. Moyle for comments on an earlier draft of this manuscript. We thank the City of Roseville, California for providing access to our research site. This work was supported by the Center for Natural Lands Management, the U.S. Fish and Wildlife Service, and the Department of Wildlife, Fish, and Conservation Biology at UC Davis.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Supplementary information on the methods used to fit hierarchical vital rate models to estimate fecundity, growth, and survival functions for *N. sipedon*. This file also contains additional details on fitting and evaluating the Integral Projection Models and size-class based matrix models.

Appendix S2. A metadata file providing information on what each data and code file contains and how to recreate the analyses presented in the paper.

Data S1. R code and data files necessary to fit the hierarchical vital rate models and to construct and analyze the Integral Projection Models for N. sipedon. R code to recreate Figures 1-5 is also included.