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Projected population persistence of eastern hellbenders (*Cryptobranchus alleganiensis alleganiensis*) using a stage-structured life-history model and population viability analysis

Shem D. Unger [a],*, Trent M. Sutton [b], Rod N. Williams [c]

[a] *Savannah River Ecology Laboratory, University of Georgia, Aiken, SC, USA*
[b] *School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA*
[c] *Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA*

A B S T R A C T

The population of eastern hellbenders (*Cryptobranchus alleganiensis alleganiensis*) in the Blue River, Indiana has undergone a dramatic decline over the last decade. Recruitment in these declining populations has been negligible, and populations are now composed almost entirely of older age classes (upwards of 20 years old). Given this dramatic decline, it is imperative to assess the impacts of these demographic patterns on population growth and long-term stability. Therefore, we developed a stage-structured, life-history model to examine the effects of varying levels of egg, juvenile, and adult survivorship on abundance, recruitment, and long-term population projections. We performed a sensitivity analysis of the model and determine which life-history parameters have the greatest potential to increase/stabilise hellbender population growth. Finally, we conducted a population viability analysis to determine the probability of extinction associated with varying management strategies. For eastern hellbender populations in Indiana, adults (especially females) are the most important component of long-term population viability. Sensitivity and elasticity analyses of the Lefkovitch matrix revealed that survival of adult and egg/larvae life-history stages are the most important for focused management efforts. Indeed, adults had the highest elasticity and reproductive value in the matrix model. Increasing survival by as little as 20% corresponded to the turning point at which the population ceased to decline and increased abundance (28% survival of egg/larvae). The importance of the transition from subadult to adult (transitional matrix element) was identified as an additional factor in maintaining abundance based on the relatively long period spent in this life-history stage (seven years for females). A population viability analysis was conducted to assess the likelihood and projected time frame of extinction for this population under no management (~25 years to complete extirpation; probability of extinction = 1) and if management efforts such as captive rearing and headstarting are undertaken (probability of extinction <0.2 at 25–30% survival of egg/larvae). Adult females had the greatest effect in reducing growth rate and population abundance when removed in exploitation simulations (91.3% versus 51.8% reduction in population growth rate), indicating translocation efforts should be designed to maintain females in the breeding pool. These models indicated that conservation management strategies aimed at ensuring the presence of adult females while concomitantly ameliorating survival at early life stages (population augmentation, translocations, introduction of artificial nest structures) are needed to stabilise the Indiana population of eastern hellbenders. This stage-structured model is the first to model eastern hellbenders and has broad implications for use across the geographic range where populations of eastern hellbenders are monitored and vital rates can be estimated.

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Introduction

Developing species-specific management strategies for long-lived species with multiple discrete life-history stages is an important challenge for conservation biologists. This difficulty is partially due to the fact that long-lived species with delayed maturation and low annual recruitment rates are particularly vulnerable to anthropogenic exploitation and extinction (Congdon et al. 1994;

* Corresponding author.
   E-mail addresses: cryptobranchus11@gmail.com,
sunger@purdue.edu (S.D. Unger).

Musick 1999). Moreover, long-lived species facing decline may exhibit high temporal variability between successful recruitment events, allowing catastrophic events to rapidly decrease their population size (Coulson et al. 2001). While population growth rates for species are usually thought to be most dependent on adult survival and reproduction (Heppell et al. 2000), there also is an increasing appreciation for the importance of juvenile survival in long-lived species (Sergio et al. 2011). For populations of long-lived species to remain stable over time, sufficient levels of reproduction and survivorship must occur at multiple life-history stages (Sibley & Hone 2002). Further, adult female survival is vital to ensure recruitment occurs over the long lifespan of iteroparous vertebrates (Eberhardt 2002). Therefore, determination of stage-dependent vital rates is essential for understanding population dynamics and planning conservation programs for imperiled species.

Stage-based matrices, such as the Lefkovitch stage-structured model (Lefkovitch 1965), are ideal for projecting population trends for long-lived species whose life histories are characterised by stage and not annual year classes (Caswell 2001; Crowder et al. 1994). In addition, stage-based model approaches also can incorporate sensitivity and elasticity analyses for identification of life-history stages which have the greatest potential to positively influence population growth rates. Stage-structured models also can be used to simulate competing conservation and management strategies focused on increasing recruitment or repatriation of adults to bolster reproduction and to prioritise management decisions (Dodd & Seigel 1991; Lubben et al. 2008).

Population viability analysis (PVA) is a method for predicting the risk of population extinction based on empirical life-history information using computer simulation (Brook et al. 2000). Such analyses are useful to either simulate the demographic effects of exploitation of individuals or supplementation efforts aimed at increasing abundance across life stages. These analyses also provide managers with objective, quantitative criteria on which decisions regarding extinction risks can be made (Armbruster et al. 1999). While stage-based models and PVAs have been used for a number of species of special conservation concern, surprisingly few have been developed for amphibians (Biek et al. 2002; Homyack & Haas 2009), many of which are facing alarming rates of decline (Griffiths & Williams 2000; Lips et al. 2005).

Eastern hellbenders (*Cryptobranchus alleganiensis alleganiensis*) are long-lived, fully aquatic salamanders found across portions of the Midwest and eastern U.S. (Petranka 1998). Many populations are experiencing declines throughout their geographic range (Wheeler et al. 2003), which is attributed to a variety of factors such as emerging infectious diseases (Briggler 2007; Souza et al. 2012), over-collection and exploitation (Nickerson & Briggler 2007), and sedimentation (Petranka 1998). Eastern hellbender declines are often characterised by a complete lack of recruitment, thus characterising survivorship of early life stages is vital as slight changes in egg and larval survival may have drastic effects for overall population growth rates (Crouse et al. 1987). In eastern hellbenders, it has been hypothesised that early life-history stage individuals may be sensitive to increased predation pressure (Gall & Mathis 2009) or may be negatively affected by increased turbidity and lower quality habitats as has been observed for the Japanese giant salamander *Andrias japonicas* (Okada et al. 2008). Clearly, factors which contribute to lower survival in the youngest life-history stages of eastern hellbenders must be understood in order to decipher the underlying changes in demography noted for declining populations of this subspecies.

Populations of eastern hellbenders within Indiana are currently confined to a 112 km stretch within the Blue River, Indiana. Several studies over the last two decades have documented not only dramatic declines in population abundance, but a general shift to a large-bodied and presumably geriatric population (Burgmeier et al. 2011; Kern 1984). If this decline continues unabated, remnant river demes within the Blue River may become increasingly fragmented and suffer reduced reproductive potential (Allee 1931; Berec et al. 2007). Repatriation (release of individuals into an area currently occupied by a species) and headstarting (HS; early life stages reared in captivity to a larger size then subsequently released) are two primary management techniques which have been used to augment amphibian populations (Dodd & Seigel 1991; Lannoo 2005). Therefore, it is essential to simulate the efficacy of repatriation of adults or subadults and headstarting programs aimed at increasing survival at early life stages for the declining population of eastern hellbenders in Indiana.

Herein, we developed a stage-structured, life-history model for eastern hellbenders in Indiana. Using this approach, our goal was to examine the effects of management aimed at increasing early life stages (eggs and larvae) of eastern hellbenders and translocation of adults and subadults on projected population dynamics of this species. The specific objectives were to utilise stage-structured modeling of eastern hellbenders in Indiana to: (1) examine the effects of varying levels of egg, juvenile, and adult survivorship on abundance, recruitment, and long-term population projections; (2) perform a sensitivity analysis of the model and determine which life-history parameters have the greatest potential to increase/stabilise hellbender population growth; and (3) conduct a population viability analysis to determine the probability of extinction associated with varying management strategies. This stage-structured modeling approach has broad-scale implications for other eastern hellbender populations with similar demographic profiles (e.g., all populations within the Ohio River drainage), and is especially relevant for current management and conservation needs considering the recent listing of the Ozark hellbender (*Cryptobranchus alleganiensis bishopi*) as federally endangered and candidate listing of the eastern hellbender subspecies for federal protection.

Methods

Study site and sample collection

Our study site, the Blue River watershed is located in southern Indiana, USA and flows 112 km until its confluence with the Ohio River near Leavenworth in southern Indiana. Land along the river corridor consists of mixed forest, agriculture, and small levels of development. River habitat consists of riffle and runs interspersed with long stretches of pooled water, and the dominant substrate types consist of a mixture of gravel, cobble, and bedrock. Sample sites within the Blue River were selected based on habitat suitability which considered stream flow type, substrate, and boulder size (Burgmeier et al. 2011).

A subset of the parameters (e.g., population size, adult, and subadult survival) used in our modeling approach were derived from previous research aimed at assessing the status of remaining hellbender populations within Indiana (Burgmeier et al. 2011; Olson et al. 2013; B. Kraus, unpublished). To obtain the data needed to parameterise stage-structured models, the eastern hellbender population within the Blue River, Indiana was monitored between July 2008 and October 2009 at 35 sites. Each site was visited with five times over a two-year period to obtain population estimates for adults by mark-recapture (MMR). Additional surveys for larvae were conducted during the summer months in 2011 and 2012 at three sites where evidence of recent breeding had been documented. Due to the increased difficulty and cryptic nature of larval and subadult age classes which occupy different habitats than adults (Nickerson et al. 2003), larval surveys consisted of hand turning potential juvenile rock shelters, primarily cobble and

smaller sized rocks. This survey technique has proven successful for finding eastern hellbender larvae in Appalachia and other stable populations (Hecht-Kardasz et al. 2012). Individual adults were collected by hand using rock flipping and snorkel-survey techniques (Burgmeier et al. 2011). All individuals were measured to the nearest 1 mm for total length (TL) and snout to vent length (SVL) using a customised restraint device (Burgmeier et al. 2010). Body mass was measured to the nearest 1 g, and PIT tags (134.2 kHz, Biomark Boise, Idaho) were inserted as unique identifiers for subsequent surveys. The probability of tag loss was evaluated using genetic techniques (individual microsatellite genotypes from a concurrent study) on a subset of the sampled population and found to be zero (Unger et al. 2012). These intensive monitoring and survey efforts provide a unique opportunity to develop a stage-structured population model based on reliable estimates of vital rate parameters specific to the Indiana population of eastern hellbenders.

General modeling approach

We used multiple population model approaches to identify which eastern hellbender life-history stages to target for future conservation management practices. The Lefkovitch matrix model was used to perform sensitivity analysis on matrix elements (e.g., survival rates, transitional probabilities, and fecundity) and is ideal for stage-structured population analysis, while the program VORTEX allows for further sensitivity analysis and projects population growth by incorporating the life-history of the species. In addition, VORTEX allows for the calculation of the probability of extinction at various survival rates. We first developed a set of population-level life-history parameters for use in our models based on data collected directly from the Indiana hellbender population and best estimates found from the scientific literature. Using these life-history parameters, we developed a series of stage-structured models in the form of a Lefkovitch matrix to examine intrinsic population growth rates (λ) under a variety of scenarios. Specifically, this model allowed us to examine the projected exponential population growth rate under a stable-stage distribution (Gotelli 2001) and perform sensitivity and elasticity analyses of specific matrix element vital rates (survivorship and fecundity) to identify which life-stage vital rates have the greatest potential to affect population growth (Caswell 2001; Crouse et al. 1987). Sensitivity and elasticity analyses on matrix elements were tested in POPTOOLS (Hood 2011), each performed as a single test on the matrix. These single matrix tests allowed us to determine how sensitive the model (intrinsic growth rate, λ) is to potential change in matrix element vital rates (sensitivity) and a proportional sensitivity (elasticity) to compare fecundity and vital rates. Lefkovitch matrix projections, however, are unable to incorporate stochasticity and matrix population projections conform to stable stage distributions. Therefore population projections for the Leflovitch model are not presented, rather the program VORTEX (Lacy et al. 2009) was used to model population growth based in the results of the Lefkovitch matrix analyses.

We used the individual-based modeling approach in the program VORTEX to both project population growth as well as perform a PVA for each projection in which we assessed the probability of extinction under low versus high survival scenarios. Specifically, we conducted a sensitivity analysis (perturbation analysis) by first finding the point of inflection (point at which population becomes positive) for egg/larvae survival. We incrementally increased survival rates of other stages individually by 5% while keeping other survival rates constant. Finally, we simulated both exploitation and captive management scenarios. To assess the vulnerability of population growth to removal of adults (exploitation), we modeled exploitation at 5% and 10% for the first five years of a 50-year simulation. In addition, to assess the difference between removal of

adult females versus adult males, we further modeled exploitation of either all females, or all males. This five-year period was chosen for two reasons, 1) model projections led to complete extirpation at longer periods and 2) this period is a realistic time frame for state management efforts. To assess the efficacy of various captive management scenarios on population growth, we modeled translocations of all three life-history stages at various levels to represent a five-year conservation management program. This time period was chosen to represent immediate efforts to prevent complete extirpation of the Indiana population.

Life-history parameters

Vital rate data (i.e., fecundity and survivorship) for models were obtained from previous research conducted on the Indiana population of eastern hellbenders (Burgmeier et al. 2011; Olson et al. 2013). For life-history traits which are poorly studied in this species, we obtained estimates from a thorough review of the scientific literature. For example, information on the proportion of females that breed each year is unknown for this population, and thus had to be based on observations of other populations (Topping & Ingersol 1981).

Survivorship curves for eastern hellbenders suggest that natural survival is low at early life stages (Nickerson & Mays 1973; Taber et al. 1975). Therefore, we set the baseline survival of early life stages (egg and larvae) at 10% which is consistent with other larval amphibian survivorship estimates (Anderson et al. 1971; Bayliss 1994; Blaustein et al. 1997). Survival rates for wild subadults are currently lacking; however, survival rates of translocated subadults were calculated to range from ~50 to 70% (Bodinof et al. 2012; J. Greathouse *pers. comms.* 2012; B. Kraus unpublished). These estimates may be lower than would be expected for wild subadults due to the additional factors associated with translocated individuals, which include dehisced sutures (Bodinof et al. 2012) or unfamiliarity with release sites (Attum et al. 2011). For this reason, we set subadult survival to 75% as older, wild subadults likely have survival rates approximating those of adults (J. Greathouse, *pers. comm.* 2012; B. Kraus unpublished). Survivorship estimates were recently calculated for Indiana adult eastern hellbenders and were accordingly set at 80% (Olson et al. 2013). Therefore, null model estimates of vital rates for the Indiana population model under no management were the following: egg/larvae survival = 10%; subadult survival = 75%; and, adult survival = 80%.

Additional parameters required for the population viability analysis included: the maximum age (35 years; Peterson et al. 1988); percent of population which is female (30%; Burgmeier et al. 2011), breeding periodicity (30%; Topping & Ingersol 1981); female age at reproductive maturity (Age 8; Nickerson & Mays 1973; Petranka 1998); breeding system (polygynous; Humphries, unpublished); sex ratio at birth (50% male; Sessions 2008; Wallace et al. 1999); density-dependent reproduction (percent breeding at carrying capacity 30%, percent breeding at low density 20%; Briggler, unpublished; Topping & Ingersol 1981); and, the percentage of males contributing to breeding (25%; Table 1; Kawamichi & Ueda 1998; Gorpurenko et al. 2006; Williams & DeWoody 2009).
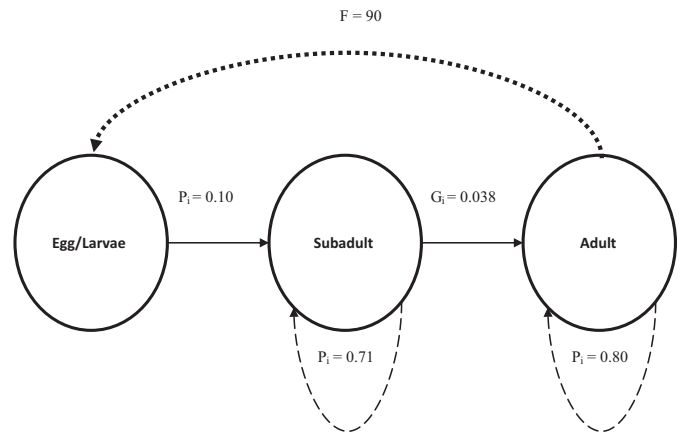
Lefkovitch matrix model

To evaluate the effects of differential survivorship at different life-history stages on population growth rates, a Lefkovitch matrix model was constructed with egg and larval stages grouped together out of necessity as information for both these stages is largely unknown (Fig. 1). A Lefkovitch matrix model is useful to examine population growth potential as it allows for matrix algebra (eigenvectors and eigenvalues) to be performed on specific elements of the matrix. Using this model, we sought to identify

Table 1
Population parameters used in VORTEX simulation models for population projection and PVA of Indiana eastern hellbenders.

Variable	Value	Source
Percent population that is female	30	Burgmeier et al. (2011)
Percent females breeding annually	30	Topping and Ingersol (1981)
Mean eggs produced by females	376	Topping and Ingersol (1981)
Female at age first maturity	Age = 8 years	Nickerson and Mays (1973); Peterson et al. (1988)
Reproductive system	Polygynous	Humphries unpublished
Maximum age of reproduction	35	Humphries unpublished; Peterson et al. (1988)
Density-dependent reproduction:		Current study
Percent breeding at low density	20	
Percent breeding at carrying capacity	30	
Survival in percent	Egg to age 1 (0.10)	Bodinof et al. (2012); Olson et al. (2013); Peterson et al. (1988); J. Greathouse, *pers. comm.*; B. Kraus unpublished
Egg to age 1	Annual Subadult survival (0.75)	
Subadult survival		
Adult survival	Annual Adult survival (0.80)	
Exploitation Adults (size: 200–600 mm)	(0.10, 0.25, 0.50)	Current study
Supplementation		Current study
Egg to age 1	200 individuals	
Subadult	20 individuals	
Adult	20 individuals (50:50 sex ratio, 2:1, 3:1 female bias)	
Extinction	Total $N < 2$	Current study
Mate monopolisation % males in Breeding pool	25	Current study
Reproductive system	Polygynous	Current study; Kawamichi and Ueda (1998); Humphries unpublished

Fig. 1. Stage-structured population model for eastern hellbenders. Standard loop diagram for life-history stages and transitions of Indiana eastern hellbenders are displayed between stages; annual survivorship (Pi; probability of staying in that stage) displayed below life stage with dashed arrows, transition probabilities (G_i; solid directional arrows), and adjusted fecundity (F) of adult stage used in matrix model (square arrow).

of a particular matrix element occurring. For example, the probability of a juvenile becoming an adult (transition element G_i) was calculated using the formula $[p_i^{di} \times (1-p_i)/(1-p_i^{di})]$, whereby p_i is annual juvenile survival and d_i is the number of years spent as a subadult (Crouse et al. 1987). The probability of remaining a juvenile (Pi) was calculated as $[(1-p_i^{di-1})/1-p_i^{di}) \times p_i]$; Crouse et al. 1987). Similarly, the matrix entry for fecundity was derived by multiplying the average fecundity (376 eggs; Topping & Ingersol 1981; Table 1) by the probability of depositing a clutch of eggs and adult survival.

Sensitivity and elasticity analysis were conducted on specific Lefkovitch matrix elements in POPTOOLS (Hood 2011) to examine the effect of incremental changes in vital rate parameters. Sensitivity and elasticity of the Lefkovitch matrix was performed each as a single test using only null vital rates (survival and fecundity; Fig. 2). Sensitivity analysis allowed us to test what the effect of changing a vital rate parameter in the model will have on overall growth rate. The elasticity analysis can quantify the proportional change in λ (Lefkovitch matrix population growth) resulting in a proportional perturbation of change in individual vital rates (Crouse et al. 1987). This analysis provides an important measure of the relative effect of individual vital rates on population growth (λ), since survival and
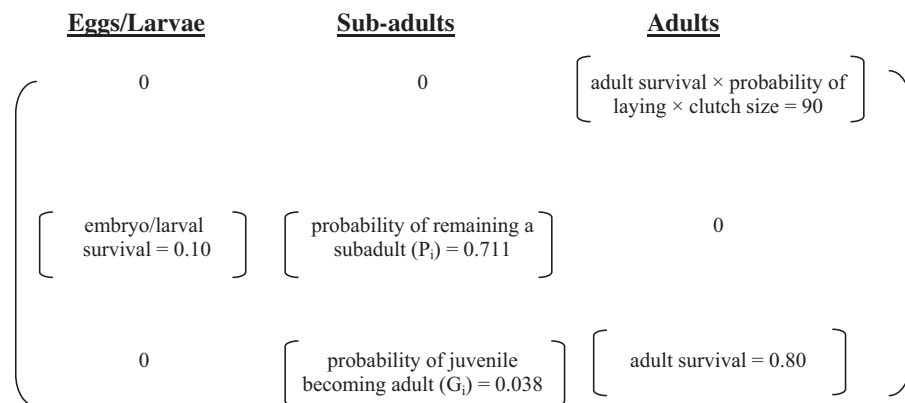
which life-history stages (egg/larval, subadult, adult) had the greatest potential to influence population growth rates. To construct specific matrix elements, we used the approach of Caswell (2001), Crouse et al. (1987), and Homyack and Haas (2009; Fig. 2), whereby survival and fecundity estimates are multiplied by the probability

Fig. 2. Leftkovitch matrix constructed for Indiana eastern hellbenders used for sensitivity analysis in POPTOOLS. Life-history matrix constructed according to Caswell (2001), Crouse et al. (1987), and Homyack and Haas (2009). The probability of a juvenile becoming an adult (transition element G_i) was calculated by the formula $[p_i^{di} \times (1-p_i)/(1-p_i^{di})]$ Crouse et al. (1987), whereby p_i is annual juvenile survival and d_i is the number of years spent as a subadult. The probability of remaining a subadult (P_i) was calculated as $[(1-p_i^{di-1})/(1-p_i^{di}) \times p_i]$ following Crouse et al. (1987). The top row corresponds to fecundity, and zeros represent matrix elements with no assigned value (i.e., no transition for adults at the last stage, no fecundity for egg/larvae or subadults).

transition rates are measured on different scales (0 to 1 for survival, and in the hundreds for fecundity; De Kroon et al. 1986). The results of sensitivity and elasticity analysis were used to determine which life-history stages to target for captive management simulations and population viability analyses (Biek et al. 2002).

To assess the potential growth rate (abundance) of the population, we calculated the dominant eigenvalue (λ) of the projection matrix in POPTOOLS. When $\lambda > 1$, the abundance increases and when $\lambda < 1$, the population declines (Caswell 2001). We also calculated the right eigenvector of the Lefkovitch matrix, which in matrix models represents a stable-stage distribution (w) and stage-specific reproductive values (v) from the left eigenvector of the matrix in POPTOOLS. The distribution (w) reveals the proportion each life-history stage comprises at the stable state, while reproductive values (v) estimate the expected per capita contribution of individuals in each life-history stage to population growth (Caswell 2001; Crowder et al. 1994). The distribution (w) can be used to compare potential population composition (percent each stage should occupy at a stable stage distribution), while reproductive values (v) can assess the relative importance specific life-history stages to reproduction.

Population projection and population viability analysis

We simulated the effects of varying survival rates for each stage on population growth using the program VORTEX (Lacy et al. 2009). This individual-based model uses Monte Carlo simulations based on species-specific population parameters (vital rates and reproductive system) to project population growth and determine the probability of extinction. This simulation software is useful because it incorporates stochastic complexity to simulations by iterating runs for population projections as well as generating standard deviations and standard errors across runs for a given simulation scenario (Lacy et al. 2009). Baseline parameters used in VORTEX were similar to the Lefkovitch matrix model: 10% egg/larvae survival; 75% survival of subadults; 80% survival of adults; and, mean number of eggs per breeding female = 376. Extinction was defined as N < 2 individuals, the point at which the population is functionally extinct. Simulations were projected for a total of 50 years and the number of iterations was averaged over 100 runs to account for stochasticity across multiple runs. We structured the starting population for VORTEX based on mark-recapture size for Blue River, Indiana survey data (N = 114 adults; Burgmeier et al. 2011).

We simulated population trends under differing levels of annual survival (10, 30, and 50%) for the combined egg/larval stage to initially assess the relative effect a 20% incremental change in early life-history stage would have on population growth. Furthermore, we determined the point of inflection (point at which the population growth rate becomes positive) for egg/larvae stages and incrementally increased other stage survival rates to assess both a target survival rate for captive management/head-starting programs and further examine the effect increasing subadult and adult survival rates. For this sensitivity analysis, the point of inflection was kept constant as subadult and adult survival were incrementally increased by 5% individually, while vital rates for other stages were kept constant. The population growth rate, end population, and percent increase from no management were calculated for each simulation. As perturbations in fecundity were found to minimally effect population growth given the overall large number of eggs for eastern hellbenders, only survival rates were perturbed in VORTEX.

The program VORTEX was also used to quantify the extinction probability for eastern hellbenders in Indiana. This program provides estimates of extinction risk by incorporating stochastic simulations based on life-history attributes of a species (Brook et al. 2000). Once parameters are entered for this program, the population is then projected over a specific time frame (50 years in this

study) over multiple runs to simulate stochasticity. Survival rates can be changed and projections can be compared for end population size, mean population growth rate over the simulation period, and the probability of extinction can be assessed for each projection (i.e., a projection of 10% egg/larvae survival can be modeled along a projection with 30% egg/larvae). This program is ideal for eastern hellbenders since it is recommended for species with long lifespan, fecundity and survival rates readily estimated, and starting populations not at a stable-age distribution (Miller & Lacy 2005). To detect a target survival rate for the egg/larval stage, the probability of extinction was simulated at incremental decreases of 5% for egg/larvae stages and compared across population projections.

Modeling exploitation and captive management

To simulate the effects of adult exploitation on population stability, we used VORTEX to run simulations with exploitation rates set at 10, 25, and 50% for adults, while other life-history stages (subadults and egg/larvae) remained constant (0) under the Harvest option for the first five years of each simulation. These exploitation rates were chosen to simulate relatively low (10%), medium (25%) and high exploitation rates (50%) which are suspected to occur historically in Indiana and similar to that observed in Missouri (Nickerson & Briggler 2007). We also examined the effects of removing a constant small number of either females or males (five individuals of one sex, ~5% starting simulation abundance) from the population during the first five years of simulations and then assessed the cumulative effect of the loss of each sex on decreasing population growth.

Captive management scenarios were simulated under the Supplementations option in VORTEX by adding varying numbers of individuals into specific life-history stage cohorts in specific years. These simulations were designed to reflect long-term successful repatriation/translocation (adults) and head-starting programs (juveniles or larvae). To test the relative effect of supplementing individuals into different life-history stages on population growth rates and final projected population sizes, realistic numbers of first-year larvae (n = 200), subadults (n = 20), and adults (n = 20) were added to population simulations annually for an initial period of five years. This short period of five years was chosen to assess the efficacy of implementing an immediate short-term program to prevent and stabilise demographic declines within Indiana. Each life-history stage was supplemented individually and only survival rates across stages and sex ratio of adults were varied. Thus, populations were supplemented for the first five years of a 50-year simulation at baseline parameters (10% survival) and then assessed with increased survival of 30% at early life stages. Initial supplementations added equal numbers of males and females; however additional supplementations were simulated to represent a female bias of 2:1 and 3:1 sex ratio (female:male).

Results

Lefkovitch matrix model

The first step to parametising our model was to assess stage-specific survival rates, subadult transitional probabilities, and fecundity of the adult life-history stage. The probability of surviving and remaining a subadult was 0.711 and the probability of a subadult transitioning to an adult was 0.038 (Fig. 2). The fecundity was 90 eggs per female per year once the adult survival rate (80%), and breeding periodicity (30%) were incorporated into the model. Of the three main matrix parameters, the subadult transitional matrix element (probability of a subadult surviving and transitioning into the adult stage) was the highest (Fig. 3). For survival
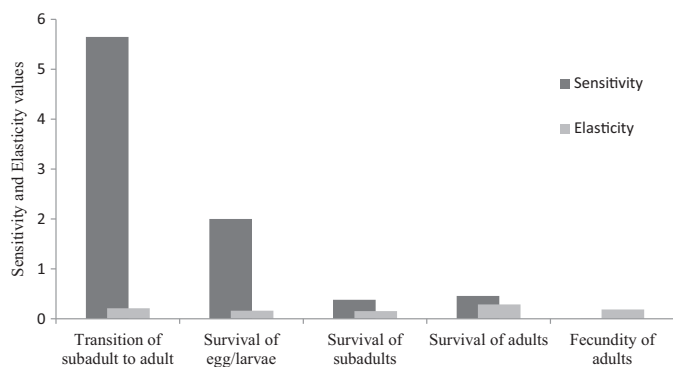
Fig. 3. Sensitivity and elasticity analyses of survival and fecundity at various life-history stages for Indiana eastern hellbenders. Note large difference in sensitivity of transition of subadult to adult followed by egg/larvae survival. The highest elasticity value was for adult survival. Dominant eigenvalue (λ) of matrix was 1.275. Calculations based on stage-structured Lefkovitch model in Fig. 2.


Fig. 4. 50-year population projection for Indiana eastern hellbenders in VORTEX with recruitment under baseline conditions with no management and survival rate set at 30%.

rate matrix elements, the sensitivity of eggs/larvae was the highest, indicating that incremental changes in survival for this stage can have a disproportionate effect on population growth (λ; Fig. 3). The second highest sensitivity value for survival was for adult life-history survival. Elasticity analysis resulted in similar values (0.168–0.283) across life-history stages for survival and fecundity with adult elasticity the highest, indicating the relative contribution of mortality rates are slightly higher for survival of adults. These results for sensitivity and elasticity of individual matrix elements (survival, transition, and adult fecundity) when taken together indicate perturbations of adult survival, followed by early life-stage survival, and finally time spent as a subadult (transitional matrix element) are the most likely to affect population growth.

The dominant eigenvalue of the matrix was $\lambda = 1.275$, indicating a highly positive growth rate potential (population potential increase by ~27% annually) under baseline conditions (10% survival of egg/larvae). The dominant eigenvalue (λ) was 1.145 and 1.045 for survival of the egg/larvae life stage set at 5% and 2.5%, respectively, illustrating the sensitivity of this stage to affect population growth at incrementally small changes in survival. The stable-stage distribution (w) for the Leftkovitch matrix indicated that the population would be dominated by egg/larvae stages (83.9%), while subadults and adults would only comprise 14.9% and 1.2% of the population, respectively. Stage-specific reproductive values (v) indicated that the average subadult will contribute 12.8 times more to future generations compared to eggs/larvae, while the average adult will contribute 189.4 times more to future generations compared to eggs/larvae. Relative stage-specific reproductive values increased the most during the transition from subadult to adult stage. The transition between subadult to adult increased reproductive value by 13.8 fold, while the transition from egg/larva to the subadult stage resulted in a 11.8 fold increase in reproductive value.

Population projection and population viability analysis

Population projections resulted in population extirpation within ~25 years, despite positive recruitment within the first 9–10 years under baseline conditions (10% survival rates of egg/larvae; Fig. 4). Changing survival for the egg/larvae life stage from a baseline of 10% to 30% resulted in stabilisation of the population and even positive growth by the end of the 50-year simulation (mean population size at year 50 = 783 individuals). There was a noticeable nadir at year 9–10 at 30% egg/larvae survival when older individuals were removed from the population, but this was followed by continued positive population growth. Mean population growth rates for 10, 30, and 50% survival of egg/larvae were r = −0.159 ± 0.019
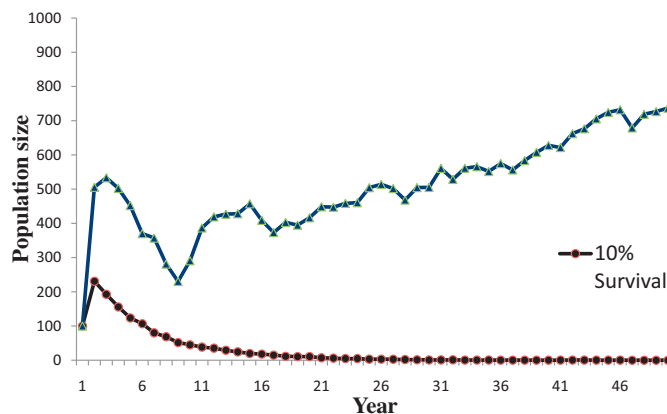
S.E., r = 0.035 ± 0.007 S.E., and r = 0.138 ± 0.005 S.E., respectively. These results indicate population growth has the potential to be positive if survival of egg/larvae is increased to ~30%, under the assumption that vital rates for other life-history stages are stable. This rate corresponded with the point of inflection (28% egg/larvae survival) which is a realistic survival rate for captive reared larvae released into rivers (J. Briggler, unpublished). Sensitivity analysis, when keeping the inflection point constant and varying other life-history stage survival rates, found that 5 and 10% increases in subadult survival resulted in higher population growth rates and greater increases in population size compared to the same increases in adult survival. Conversely, increases of 15 and 20% for subadult and adult survival resulted in similar increases in population size and growth rate (Table 2).

Simulations of the viability of the Indiana population indicate probable extinction within 25 years unless aggressive management strategies are implemented. Mean time to extinction across runs (P [Ext] = 1; 16 years) was lower at baseline conditions (10% survival of egg/larvae). Increasing survival of egg/larval stage to 30% (found to be close to the inflection point of 28%) resulted in no extinctions across all runs (P [ext] = 0; Fig. 5).

Modeling exploitation and conservation management

Using exploitation values of 10, 25, and 50% for the adult life stage, complete population extirpations occurred within 15, 13, and
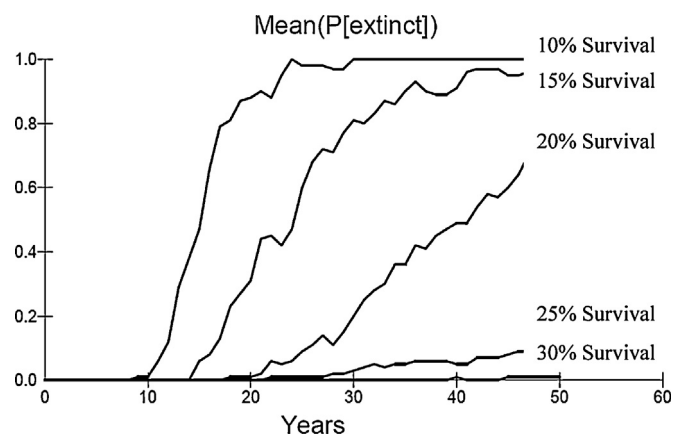
Fig. 5. Probability of Indiana eastern hellbender population extinction at incremental stages of survival rates for egg/larval stage in VORTEX. Note increasing survival at this stage to 25–30% results in low probability of extinction.

Table 2
Sensitivity analysis performed in VORTEX. The point of inflection (point at which population growth becomes positive) for egg/larvae stage was kept constant at 28%. Subadult and adult survival rates were then incrementally increased at 5% intervals to measure their relative contribution to population growth, population size at the end of 50-year simulation, and fold increase in population size compared to no increase.

Percent increase in survival	Subadult			Adult		
	Population growth rate	End population size	Increase (fold)	Population growth rate	End population size	Increase (fold)
Increase 5%	0.057	1975	4.42	0.043	1060	2.37
Increase 10%	0.091	8661	19.37	0.070	3727	8.34
Increase 15%	0.122	9931	22.22	0.094	9312	20.83
Increase 20%	0.151	9985	22.34	0.118	9903	22.15

Table 3
Simulated translocation scenarios across eastern hellbender life-history stages. Supplementations occurred only during the first five years of 50-year runs to model a five-year management program. The mean annual population growth rate, population size at the end of 50-year simulation, and percent increase in final population size from not supplementing (no management) are reported under each supplementation scenario. All simulations performed in VORTEX.

Supplementation Scenario	Annual pop. growth rate (r)	Population size at 50 years	% increase in final population size
200 one-year-old	0.047	1236	68%
20 subadults	0.046	1209	42%
20 adults	0.055	1573	124%
20 adults (female bias 2:1)	0.058	1960	197%
20 adults (female bias 3:1)	0.061	2219	220%

8 years, respectively. The relative effect of removing females was nearly two times greater than males. For example, the removal of five adult females for the first five years of simulation caused the population to become extinct 14 years sooner compared to a similar removal scenario for males. Removing females under this scenario resulted in a 91.3% reduction in population growth rate compared to a 51.8% reduction following the removal of males.

Simulations of stock supplementation (repatriations) exhibited relatively negligible effects if carried out for a short period (five years) even with relatively large levels of compensation; i.e., either adding 200 larvae greater than age 1, 20 subadults, or 20 adults per year under baseline conditions (10% survival of egg/larvae). However, a five-year supplementation when combined with an increase in annual egg/larval survival (at the 30% egg/larval survival threshold) resulted in increasing population numbers at the end of the 50-year simulation. Over the 50-year supplementation period, adding 200 age 1 larvae resulted in an increase in abundance (mean growth rate) of $r = 0.047 \pm 0.006$ S.E. which was similar to that realised by adding 20 subadults ($r = 0.046 \pm 0.006$ S.E.), but smaller than that realised by adding 20 adults ($r = 0.055 \pm 0.005$ S.E.; Table 3). Moreover, for the same time frame, supplementing the population with 20 adults more than doubled the final population size (124% increase), whereas supplementing with subadults or larvae resulted in 42% and 68% increase in the final population size, respectively. Supplementations with a 3:1 female bias exhibited the highest mean growth rate overall ($r = 0.061 \pm 0.005$ S.E.) and a 220% increase in final population size versus a 2:1 female bias ($r = 0.058 \pm 0.005$ S.E.; 197% increase) for the same period (Table 3).

Discussion

We used various methods (matrix model, population projection, and PVA) to simulate the trajectory for the Indiana eastern hellbender population. We initially determined which life stages are likely to respond to management and then simulated the effect exploitation and conservation-management strategies would have on population growth. The results of this multi-modeling approach indicate that the most effective means to prevent extirpation is to concomitantly maintain adult female presence, given their high reproductive value, followed by increasing survivorship of early life-history stages. The relatively high adult and subadult survival rates for eastern hellbenders demonstrate the importance of older life-history stages, since it is expected that early life history stages are unlikely to survive. This finding is consistent with expectations for long-lived, iteroparous species (Congdon et al. 1994; Eberhardt 2002). Further, the high sensitivity value for the subadult life-history stage transition indicate the relatively long time spent in this stage (age at reproduction for females is age 8) is important for maintaining abundance. However, the low elasticity value for subadults indicates this may be an artifact of the long period spent in this stage (seven years).

It is clear that a model or simulation is limited by its parameters and their reliability in predicting population growth and extinction probabilities (Coulson et al. 2001; Galimberti et al. 2001). For example, some caveats for the Leftkovitch modeling approach include the fact that only females are included, individuals within each life-history stage behave similar regardless of their age, size and genetic make-up, and have the same vital rates within stages (Caswell 2001). Further, abundance growth rates used in these models should be interpreted as potential abundance growth rates subject to demographic pressures (e.g., predation, etc.) and environmental stochasticity. However, a real strength of this study is that simulations were largely based on empirical data collected within Indiana, a population monitored for nearly a decade.

A primary important finding of this study was indicated by the elasticity for adult survival. A slight reduction in adult survival is likely to reduce population abundance, a pattern that is supported by the results of the exploitation simulations. The importance of adult presence, especially females, is further indicated by the high reproductive value (v) for adult females (189.4). The reliance on adult female presence is consistent with other studies in long-lived species, such as desert tortoises and turtles (Enneson & Litzgus 2008; Reed et al. 2009), snakes (Hyslop et al. 2011), and sturgeon (Jaric et al. 2010). Therefore, management efforts should place high priority on both assessing adult presence and determining sex ratios to maintain adequate number of individuals within Blue River stream reaches. Minimising stressors to the adult life-history stage, such as decreasing predation, harvest, and improving water quality is recommended. Future studies should assess the minimal relative abundance within sites to overcome the Allee effect and increase reproduction.

The Lefkovitch stage-based model indicated the potential for highly positive population growth (λ). If survival rates of the egg/larvae life stage in the field are lower than our conservative estimate of 10%, then this population has a lower rate potential for abundance increases. The stable-stage distribution (w) predicted populations would need to be composed of a large number of larvae in a given year to be stable. Larval life stages of the eastern hellbender have not been documented in Indiana since at least before 1984 (Burgmeier et al. 2011; Kern 1984). One explanation is that other factors, such as high predation, are likely affecting survival of the early life-history stages of this species. Known predators of

eggs and larvae include fish, water snakes, as well as adult hell-benders (Nickerson & Mays 1973; Smith 1907). Further, if adults were historically harvested causing reduced abundances within river demes, then over time this reduction in adult individuals could decrease local reproduction and thus recruitment. Alternatively, the lack of larvae within our study site could be due to the difficulty in detecting larvae which are difficult to detect even at higher densities and are known to occupy the interstitial matrices of gravel/cobble habitats (Nickerson et al. 2003; Hecht-Kardasz et al. 2012). The difficult in detecting larvae is further exemplified given targeted surveys in areas of recently documented nests have found no larvae in these same habitats within Indiana presumably due to low densities or increased predation. Moreover, because we utilised similar techniques for our larval surveys which in other populations have detected the presence of both gilled larvae and juveniles, the lack of recruitment in the Blue River population warrants further investigation. The Indiana population notwithstanding, this relatively high potential for growth and the stable-stage distribution (w) indicate stable populations should be composed of a larger percentage of egg/larvae in any given year. Indeed, there are hellbender populations that appear to represent "stable" populations, such as the Little or Hiawassee rivers in Tennessee, where ∼50% of the population is made up of gilled larvae (Nickerson et al. 2003; M. Freake, *pers. comm.* 2011) and support matrix model predictions of the stable stage distribution (w) indicating a high percentage of population composed of egg/larvae.

The likelihood for lower survivorship of early life stages in Indiana was consistent with our sensitivity analysis which revealed survival of egg/larvae is highly sensitive to decreases in survival rate. Thus, the intrinsic growth rate (λ) is heavily influenced by slight perturbations in egg and larval survival, time spent as a subadult, and adult female presence. The high sensitivity we observed for egg/larvae survival is similar to other studies in birds (Fefferman & Reed 2006), mammals (Mcleod & Saunders 2001), toads (Aubry et al. 2010), and other salamander species (Zambrano et al. 2007). The results of this study are encouraging since at 30% egg/larval survival, the overall population growth rate remains high, indicating the potential for positive population growth following implementation of management strategies focused on head-starting and translocations. However, any conservation management efforts should focus on maintaining presence of adult females to ensure breeding, and thus potential recruitment of early life-history stages occur.

The results from inflection point sensitivity analysis identified subadult increases in survival of 5–10% to have a greater effect than increasing adult survival by the same percentage. This may be in part due to the lower survival rate of subadults (75%) versus adults (80%) under the null (no management) scenario. This result is consistent with the high sensitivity value for the transitional stage for subadult to adult. It is likely that a lack of recruitment of early life-history stages or increased predation by aquatic predators, such as river otters known to occur within Indiana sample locations are affecting this life-history stage (B. Kraus, *pers. comm.* 2012). However, at present, the effect of river otter (*Lontra canadensis*) predation on either the subadult or adult life-history stage is unknown. Translocations with subadults may be warranted if individuals are available (i.e., possibly from captive rearing programs), especially if they are larger individuals approaching the transition to adult stages. Head-starting programs which reduce the time spent at this transitional life-history stage potentially enabling subadults to become sexually mature sooner should also be considered. Management efforts which focus on re-establishing healthy adult stocks while simultaneously protecting subadults may restore declining populations more effectively (Heppell & Crowder 1998).

Many state agencies (including Indiana) are indeed relying on repatriations, translocations, and head-starting programs as viable management strategies to reverse population declines across the country. While it is unknown how many individuals are ideal for translocations, herpetological repatriation programs which release more individuals have higher success rates (Germano & Bishop 2008). Moreover, results from this study and others (Coates & Delehanty 2006; Faust et al. 2004; Holmes 2008; Lewis et al. 2012) suggest that to maximise population growth, translocation programs should focus on increasing the number of adult females. Indeed, simulations from this study show a 40% reduction in population growth with concomitant decreases in adult females. Therefore, management programs aiming to increase the rate of population growth and reduce demographic stochasticity should increase female bias to 2:1 or 3:1 (Armstrong & Ewen 2001; Wedekind 2012). While the primary focus of conservation efforts should be on protecting habitat, our model results suggest that adults, especially females, are an important component of long-term population viability. Model results also indicate that head-starting programs that increase the survivorship of younger age classes to levels approaching 30% have the potential for positive, long-term population growth and viability. Preliminary data suggest that head-starting programs in which larvae are reared for a period of one year increase survival of early life stages to 30% (J. Briggler, unpublished). Further, increasing the nesting habitat for adults by adding artificial nest structures in Indiana similar to conservation efforts in Missouri (Briggler & Ackerson 2012; B. Kraus, unpublished) may facilitate the availability of breeding habitat and collection of eggs for head-starting.

While having a protracted life history allows wildlife managers to utilise adult individuals within the next decade, the delayed sexual maturation and long period within the subadult stage may place eastern hellbenders at further risk for extinction. Indeed, for Indiana hellbender populations, if management strategies are not implemented to ensure the presence of adults, especially females, to bolster egg/larval survival, viability analyses predict a high probability for extinction within one to two decades. Future studies should therefore assess translocation densities necessary to increase breeding, along with determining habitat and diet requirements for the larval stage of eastern hellbenders. These additional studies will enable population specific demographic data for future modeling and population projection within Indiana as well as across the geographic range of eastern hellbenders.

This study is the first to model a well-studied eastern hellbender population while simultaneously performing sensitivity analyses and a PVA to inform future conservation and research efforts. While some demographic data are still lacking (e.g., information on survival of early life stages), these models provide a tractable method for predicting population trends which can be applied to conservation management in other eastern hellbender populations. This is especially important as roughly half the species' range (predominantly within the Ohio River drainage) is experiencing similar demographic patterns of declines (Foster et al. 2009; Phillips & Humphries 2005).

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