

ARTICLE

Concurrent threats and extinction risk in a long-lived, highly fecund vertebrate with parental care

George C. Brooks  | William A. Hopkins | Holly K. Kindsvater

Department of Fish and Wildlife
Conservation, Virginia Tech, Blacksburg,
Virginia, USA

Correspondence

George C. Brooks
Email: boa10gb@vt.edu

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Abstract

Detecting declines and quantifying extinction risk of long-lived, highly fecund vertebrates, including fishes, reptiles, and amphibians, can be challenging. In addition to the false notion that large clutches always buffer against population declines, the imperiled status of long-lived species can often be masked by extinction debt, wherein adults persist on the landscape for several years after populations cease to be viable. Here we develop a demographic model for the eastern hellbender (*Cryptobranchus alleganiensis*), an imperiled aquatic salamander with paternal care. We examined the individual and interactive effects of three of the leading threats hypothesized to contribute to the species' demise: habitat loss due to siltation, high rates of nest failure, and excess adult mortality caused by fishing and harvest. We parameterized the model using data on their life history and reproductive ecology to model the fates of individual nests and address multiple sources of density-dependent mortality under both deterministic and stochastic environmental conditions. Our model suggests that high rates of nest failure observed in the field are sufficient to drive hellbender populations toward a geriatric age distribution and eventually to localized extinction but that this process takes decades. Moreover, the combination of limited nest site availability due to siltation, nest failure, and stochastic adult mortality can interact to increase the likelihood and pace of extinction, which was particularly evident under stochastic scenarios. Density dependence in larval survival and recruitment can severely hamper a population's ability to recover from declines. Our model helps to identify tipping points beyond which extinction becomes certain and management interventions become necessary. Our approach can be generalized to understand the interactive effects of various threats to the extinction risk of other long-lived vertebrates. As we face unprecedented rates of environmental change, holistic approaches incorporating multiple concurrent threats and their impacts on different aspects of life history will be necessary to proactively conserve long-lived species.

KEYWORDS

conservation, eastern hellbender, extinction debt, filial cannibalism, life history, population dynamics

INTRODUCTION

Detecting declines of long-lived, highly fecund vertebrates, including some fishes, reptiles, and amphibians, can be challenging (Cox et al., 2022; McRae et al., 2017). Long-lived species with high fecundity exhibit a mixture of fast and slow life history traits, thereby preventing a boilerplate evaluation of extinction risk (Hutchings et al., 2012). The imperiled status of long-lived species can often be masked by extinction debt, wherein adults persist in habitats that no longer support viable populations, and environmental perturbations or demographic shifts that undermine population viability may often go unnoticed for decades (Kuussaari et al., 2009; Tilman et al., 1994). Large clutch sizes can in theory provide resilience to extinction for such taxa, but low survival of larval stages and density-dependent recruitment often represent a key bottleneck that limits a species' recovery potential (Alford & Richards, 1999; Pechmann & Wilbur, 1994; Reynolds et al., 2005; Wilbur, 1980). In addition, species with complex life histories (such as distinct larval and adult stages, explosive breeding, or parental care) will often experience density dependence at multiple life stages, further reducing the capacity of populations to rebound from declines (Biek et al., 2002; Congdon et al., 1994; Crouse et al., 1987; Schmidt et al., 2005; Vonesh & De la Cruz, 2002). Density-dependent processes will persist even in small or declining populations if the availability of nest sites or larval refugia have been reduced following habitat alteration. If such nuances are not incorporated into the demographic models traditionally used to evaluate population viability, the vulnerability of species to local or global extinction can be underestimated (Anderson et al., 2017; Congdon et al., 1994; Ono et al., 2019). As a result, long-lived, highly fecund vertebrates may escape the attention of conservation scientists until populations have already surpassed a tipping point (de Silva & Leimgruber, 2019; d'Eon-Eggertson et al., 2015).

Conservation efforts are further complicated by the multiple ongoing threats to biodiversity (Greenville et al., 2021; Isaac & Cowlishaw, 2004; Kimmel et al., 2022). Traditional population viability analyses typically seek to identify the most sensitive life stage to environmental perturbations in order to identify management priorities, yet it is ultimately the combination of threats and their overall impact that will determine population growth rate (Beissinger & McCullough, 2002). Different threats can impact different stages of an organism's life history, and vulnerability to particular threats strongly depends on a species' ecology (Brooks & Kindsvater, 2022; Isaac & Cowlishaw, 2004; Reynolds, 2003). For example, in sea turtles, the dominant threats posed to early life stages

(e.g., nest predators, beach traffic, artificial lights) are completely different from the primary threats to adults (e.g., boat collisions, fishing bycatch; Bolten et al., 2011; Donlan et al., 2010). Similarly, in pond-breeding amphibians, an increased frequency of droughts is likely to reduce recruitment success (Crawford et al., 2022; Taylor et al., 2006), whereas deforestation impacts the survival of terrestrial juveniles and adults (Todd et al., 2014). Clearly, for the effective conservation and recovery of species in the modern era, multiple novel threats experienced across a species' life history must be identified and evaluated.

The eastern hellbender (*Cryptobranchus alleganiensis*, hereafter hellbender) exemplifies the challenges associated with population assessments of long-lived, highly fecund vertebrates that simultaneously face multiple anthropogenic threats. Hellbenders are fully aquatic salamanders in the family Cryptobranchidae that live up to 30 years and produce hundreds of eggs each year after reaching sexual maturity (Petranka, 1998). Historically, hellbenders inhabited streams across 15 states in the eastern United States, but they have experienced rapid local extirpations throughout their range (Jachowski & Hopkins, 2018; USFWS, 2018; Wheeler et al., 2003). Population declines are often associated with loss of upstream riparian forest cover and characterized by a shift in age class distribution where small populations are primarily composed of old adults, with little evidence of recruitment of young age classes (Jachowski & Hopkins, 2018; Wheeler et al., 2003). One hypothesis for this pattern is a reduction in the number of suitable nesting sites under boulders due to high siltation caused by upstream deforestation. Alternatively, nest sites may be plentiful, but conditions in the stream may elevate rates of nest failure or larval mortality or increase the strength of density-dependent interactions of larvae due to siltation of their microhabitat. Hellbenders are particularly interesting in this regard because they exhibit extended parental care of eggs and larvae (Hopkins et al., 2023), which in theory could improve the fate of nests and increase early larval survival. However, attending males also exhibit whole-clutch filial cannibalism (Hopkins et al., 2023). Lastly, some experts have noted concerning rates of adult mortality as a result of fishing and/or collection for the pet trade (Nickerson & Briggler, 2007; USFWS, 2018). These hypotheses are not mutually exclusive; some combination of these threats may be generating the observed declines (Burgmeier et al., 2011; Foster et al., 2009; Hopkins et al., 2023; Jachowski & Hopkins, 2018; Unger et al., 2013; USFWS, 2018).

Here we develop a demographic model to understand how multiple co-occurring threats impact the population viability of a long-lived, highly fecund vertebrate with

parental care. We simulate the age-structured population dynamics of hellbenders using recent data on reproductive ecology collected from artificial nest boxes (Hopkins et al., 2023). Our parameterization explicitly models the fates of individual nests and includes multiple sources of density-dependent mortality—one during the egg and hatchling stages experienced within nests and another for free-swimming larvae following emergence from nests. We explore scenarios with (1) limited nest site availability, (2) increased rates of nest failure, (3) a range of strengths of density dependence in juvenile survival rates, and (4) stochastic adult mortality. In each scenario, we quantify extinction probabilities and compare our predictions to recent evidence for changes in age class structure within declining populations (Jachowski & Hopkins, 2018). We interpret our findings in the broader context of detecting declines in long-lived vertebrates with parental care and discuss how our approach can be generalized to evaluate the population viability of species facing multiple concurrent anthropogenic threats.

METHODS

Study species

Hellbenders exhibit a suite of life history traits that are typical of many long-lived, highly fecund vertebrates. Individuals grow to a maximum length of approximately 570 mm (Taber et al., 1975; Wiggs, 1976), and both sexes can live for 30 years (Browne et al., 2014; Makowsky et al., 2010; Peterson et al., 1983; Taber et al., 1975). Males reach sexual maturity at 4–6 years of age, whereas females mature at 5–7 years of age (Figure 1c; Nickerson & Mays, 1973; Peterson et al., 1983; Taber et al., 1975; Topping & Ingersol, 1981). Hellbender clutch sizes generally range from 100 to 600 eggs (>90% of clutches observed in wild populations fall within this range; Hopkins et al., 2023), and the number of eggs produced by females is positively correlated with their body size (Smith, 1907; Topping & Ingersol, 1981).

Hellbenders nest under large boulders in the streams they inhabit and exhibit obligate paternal care with males guarding clutches and larvae for approximately 8 months (Hopkins et al., 2023). Caring male hellbenders exhibit filial cannibalism, where they consume some or all of their clutch. Filial cannibalism is presumably a natural behavior in hellbenders, as it is relatively common in species with obligate paternal care (Klug et al., 2006; Klug & Bonsall, 2007; Manica, 2002). However, recent evidence from studies of hellbenders nesting in artificial shelters suggests that nest failure rates are highest at sites with low riparian forest cover and that whole-clutch filial cannibalism is the

most common reason for nest failure at these sites (Hopkins et al., 2023). The relative influences of nest success, nest site availability, and recruitment on population viability of hellbenders is unclear. It is likely that the longevity of adults can buffer populations against diminished reproductive returns (Chesson, 1984; Chesson & Warner, 1981; Taylor et al., 2006), but to what degree is unknown. To answer these questions in a modeling framework, we used specific relationships regarding growth, mortality, and size-dependent fecundity to understand the connection between demographic structure and viability.

Growth and mortality

We used published estimates of somatic growth rates for adult hellbenders to relate total length (millimeter) to age (years) with a von Bertalanffy growth curve (Bodinof et al., 2012; Smith, 1907; Unger & Mathis, 2013). We assumed that both sexes grow at equal rates, achieve the same asymptotic body size, and experience the same size-dependent mortality rates (Figure 1b). We assume individuals face a density-dependent bottleneck in survival during the first years of life after emergence, as young-of-the-year presumably must compete for hiding spaces and food. Although there is limited information on density-dependent processes in wild populations, siltation is often touted as the biggest threat to hellbender habitats (USFWS, 2018); siltation is likely to impact populations by reducing nest sites and larval habitat, and thus we expect density-dependent survival early in life to be an important consideration even in small and declining populations. We modeled survival to the end of the juvenile period as a saturating function of density, following the Beverton-Holt recruitment function commonly used to represent recruitment of larval stages (Table 1; Kindsvater et al., 2016). We assumed an equal sex ratio at recruitment based on prior studies (Humphries & Pauley, 2005; Peterson et al., 1988), although male-skewed sex ratios have been documented in some populations (Burgmeier et al., 2011; Foster et al., 2009; Hillis & Bellis, 1971; Smith, 1907). At age one, we assume individuals were 100 mm long (Peterson et al., 1983; Smith, 1907; Taber et al., 1975). From Year 1 onward, we modeled hellbender survival as a function of size that increased asymptotically following the survivorship curves provided in Taber et al. (1975), Peterson et al. (1983, 1985), and Olson et al. (2013) (Figure 1b).

Reproduction and nest fates

Our model incorporates several key aspects of the reproductive biology of hellbenders: size-based maturation and

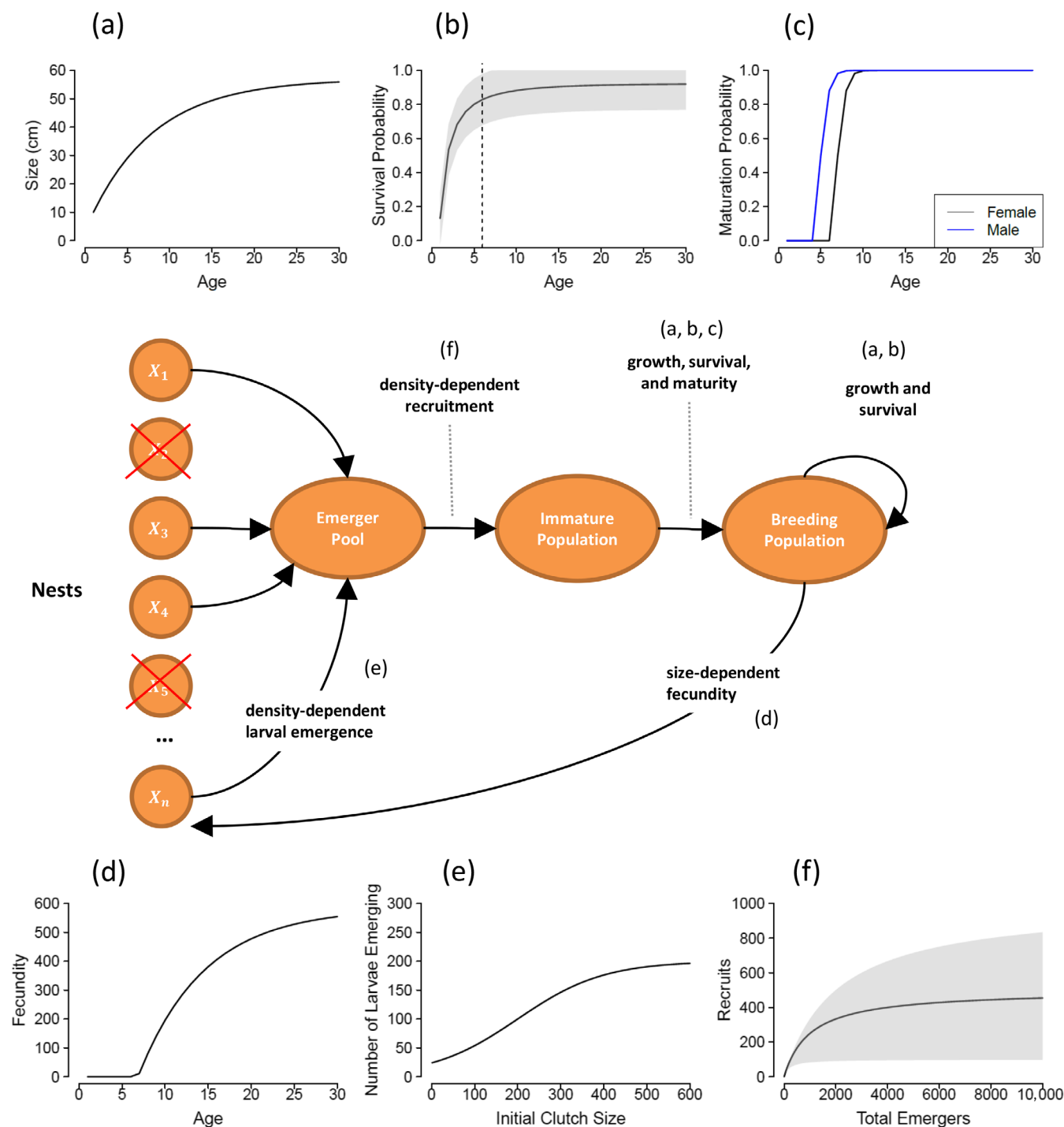


FIGURE 1 Modeled hellbender life cycle with associated vital rate functions. Nests are modeled individually, and females deposit one clutch per nest site such that the number of nest sites limits the number of clutches that can be deposited in a given year. X_n represents the clutch size deposited in nest site n in any given year, and red crosses indicate nests that fail in that year. Panels in top row describe functions for size-dependent growth (a), survival (b), and maturation (c). Panels in bottom row describe the relationship between clutch size and female body size (d), the relationship between initial clutch size and number of larvae emerging from nests (e), and the strength of density-dependent recruitment (f). For models that include stochasticity in survival and recruitment, the range of values drawn from is indicated by the shaded region (b, f).

fecundity (egg production), varying availability of nest sites, and varying nest fates. We assume that individuals mature as a probabilistic function of age and that annual

egg production depends on female body size (Figure 1d). We model clutches individually to incorporate hellbender-specific nesting behavior and characterize

TABLE 1 Population model functions and their interpretation.

Process	Equation	Interpretation
Von Bertalanffy growth function	$L(a+1) = L(a)e^{-k} + L_{\infty}(1 - e^{-k})$	L_{∞} and k determine size L at age a
Maturation probability function	$p_m(a) = \frac{1}{1 + e^{-q(a - a_{mat})}}$	Function describing cumulative probability (ogive) individuals will be mature at age a ; a_{mat} is age at which 50% of individuals mature; q determines steepness of sigmoidal curve
Size-dependent fecundity	$f(a) = mL(a) - c$	Fecundity depends on length, which depends on age; size-specific fecundity parameters are m and c
Initial number of eggs per nest site, incorporating nest failure	$X_n(t) = f(a) \times \text{Bernoulli}(1 - p_{\text{fail}})$	Size of clutch deposited in nest site n at time t is modeled as a function of the size of the female assigned to nest site n . Assignments are drawn at random from the pool of mature females, and nests fail with probability p_{fail}
Density-dependent larval emergence	$P_n(t) = \frac{K}{1 + e^{-r(X_n(t) - K)}}$	Where $P_n(t)$ is number of larvae emerging from nest n at time t , with relationship between initial number of eggs in a nest and number of larvae emerging modeled as a logistic curve with parameters K and r
Density-dependent recruitment	$N_0(t+1) = \frac{\alpha \sum P_n(t)}{1 + \beta \sum P_n(t)}$	Beverton-Holt recruitment function
Size-dependent instantaneous mortality rate	$M(a) = M_u L(a)^b$	Following Lorenzen (1996), size-specific mortality parameters are M_u and b . This function is used to calculate the survival function in Figure 1b
Population dynamics through time	$N(a+1, t+1) = \begin{cases} N_0(t) & \text{if } a=0 \\ N(a, t)e^{-(M(a)+F(a))} & \text{if } a>0 \end{cases}$	$N(a, t)$ is number of individuals age a alive at time t . Survival to the next time step is determined by size-specific (age-specific) natural mortality rate, $M(a)$, and harvest $F(a)$. $N_0(t)$ is made up of equal numbers of males and females

individual nest fates. We assume that hellbender population dynamics within a stream can be represented by a core subpopulation that roughly corresponds to a 1-km reach and explore scenarios where nest sites are severely limited by siltation (nest sites <5) and scenarios when nest sites are plentiful in that area (Hopkins et al., 2023; Jachowski & Hopkins, 2018; USFWS, 2018). We arbitrarily set an upper bound of 30 nest sites because exploratory analyses showed that increasing nest site availability further had minimal impact on population trends, owing to the density-dependent mortality experienced by larvae after emergence (Appendix S1: Section S3). In our model, females are randomly assigned to a nest site. If there are more females than nest sites in a particular year/scenario, females that are not assigned to a nest site do not breed in that year. For simplicity, we did not consider size-based competition among males or females for access to nest sites, or the case where multiple females laid clutches at the same nest site. Each female that is assigned to a nest site deposits a clutch of eggs, and the size of the clutch is determined by the body size of the female (Figure 1). Because hellbenders exhibit obligate paternal care, all clutches laid are randomly assigned

to a male; if there are fewer males than clutches in a given year/scenario, clutches not assigned to a male are eliminated. We assume, based on recent work (Hopkins et al., 2023), that paternal care behavior and the probability of cannibalism of eggs do not vary among males of different sizes or ages.

Larval emergence

After a clutch is laid in early autumn, it takes 8 months for surviving hellbender larvae to emerge. The caring male occupies the nest site over winter; based on empirical observations, male presence appears to be essential for nest success. Observations of wild populations have documented nest failure due to predation, abandonment, environmental factors such as flooding, or whole-clutch cannibalism by parental males (Hopkins et al., 2023). The proportion of failing nests varies considerably across populations (Hopkins et al., 2023); therefore, we considered a range of nest failure rates in our model scenarios. In each scenario, a random sample of nests is assumed to fail and removed from the population before emerging

larvae are pooled and subjected to density-dependent recruitment (Figure 1f). The proportion of nests that fail varies with the background rate of nest failure p_{fail} (Table 2); the number of larvae that die with the loss of a nest varies depending on the size of the female that laid a clutch at that nest site. Recent empirical evidence suggests the number of larvae emerging from nests is positively correlated with initial clutch size in small clutches but shows no relationship in large clutches

(Hopkins et al., 2023). We therefore modeled the number of emerging larvae per nest as an asymptotic function of the number of eggs laid in a successful nest (Figure 1e).

Modeling framework

We developed a size- and age-structured population model that included the key aspects of the hellbender life

TABLE 2 Modeled life-history parameters and their sources.

Parameter	Definition	Value	Females	Males	Source ^a
Growth and mortality parameters (equations in Table 1)					
M_u	Natural mortality rate scale coefficient	500			Values were chosen to approximate results from Taber et al. (1975), Peterson et al. (1983, 1985), and Olson et al. (2013)
b	Natural mortality rate coefficient, drawn from uniform distribution	$b \sim U(-1.3, -1.4)$			Values were chosen to approximate results from Taber et al. (1975), Peterson et al. (1983, 1985), and Olson et al. (2013)
p_{fail}	Bernoulli probability of nest failure	0–1			A range of values was considered
A_{max}	Maximum age (years)	30			Taber et al. (1975), Peterson et al. (1983), Browne et al. (2014)
L_{inf}	Asymptotic size in von Bertalanffy growth function (millimeters)	570			Taber et al. (1975), Wiggs (1976)
k	Growth coefficient in von Bertalanffy growth function	0.13			Smith (1907), Bodinof et al. (2012)
L	Length-at-age; $L(1)$ is reported here as size at emergence (millimeter)	100			Smith (1907), Taber et al. (1975), Peterson et al. (1983)
Reproduction parameters					
a_{mat}	Coefficient of maturation function that determines age where 50% of individuals mature; varies according to sex i		7	5	Taber et al. (1975), Topping and Ingersol (1981), Peterson et al. (1983)
q	Shape coefficient of age-based maturation		2	2	Values are based on ranges in Taber et al. (1975) and Peterson et al. (1983)
m	Slope of size-dependent fecundity function		3.025	...	Topping and Ingersol (1981)
c	Intercept of size-dependent fecundity function		1141	...	Topping and Ingersol (1981)
r	Slope of larval emergence function	0.01			Hopkins et al. (2023)
K	Asymptote of larval emergence function	200			Hopkins et al. (2023)
α	Slope near origin of recruitment function	0.5			Arbitrary
β	Parameter of Beverton-Holt recruitment function; asymptote will be at α/β	0.0001–0.005			A range of values was explored (Figure 4)

^aArbitrary values were varied in sensitivity analyses and do not qualitatively affect conclusions.

cycle described earlier. Our approach was based on a model of population demography and growth of fishes with obligate paternal care in Kindsvater et al. (2020), which itself was adapted from the models commonly used in stock assessments of fished populations (Mangel, 2006). However, we significantly expanded the scope of this previous model to include biologically realistic processes that could affect hellbender population dynamics, such as variation in the availability of appropriate nest sites, two sources of density-dependent mortality in early life stages, loss of adults from the breeding population, and environmental stochasticity (Figure 1). Our approach is distinct from that of previous assessments of hellbender population dynamics, which assumed a fixed proportion of larvae grew into juveniles, resulting in exponential population growth (Unger et al., 2013). We started from an arbitrary population size (100 adults and 1000 juveniles) and allowed the population to equilibrate and reach a stable age distribution, representing a plausible baseline for its historic age structure and size. After emerging from the nest, juveniles spend the rest of the year at large before recruiting to the age-structured population, a process represented with a density-dependent recruitment function (Table 1). We projected population dynamics under different scenarios representing the individual and interactive effects of nest site availability, nest failure predominantly due to filial cannibalism, and variability in adult mortality, in order to understand their relative contributions to population demography and viability into the future. All functions and parameters representing each process are in Tables 1 and 2. All models were programmed in R (R Core Team, 2023), and the code needed to reproduce the analysis is archived on Zenodo (Brooks et al., 2023).

Deterministic simulations

We first simulated populations with rates of nest failure ranging from 0% to 80% and allowed each population to reach equilibrium. Because nest failure in artificial cavities can reach 100% in degraded sites (Hopkins et al., 2023), we then increased the nest failure rate for each scenario to evaluate the demographic consequences of chronic recruitment failure. To isolate the effect of nest failure rates on population growth, we assumed that nest sites were not limiting ($n = 30$), and adult survival was constant in these initial scenarios. Specifically, the b parameter in the size-dependent mortality function was fixed at -1.38 (Table 1). Further, we treated juvenile survival and recruitment rates as fixed parameters in order to investigate deterministic population dynamics and demography. Specifically, the α and β parameters of the

Beverton-Holt recruitment function were set to 0.5 and 0.001, respectively (Table 1). Essentially, this approach assumes that spatial and temporal variation average out over the total population, such that mean parameter values provide good approximations of the fate of a given cohort. To explore the contributions of density dependence at different life stages, we compared simulations with and without density-dependent larval emergence and with and without Beverton-Holt recruitment.

Stochastic simulations

Environmental and demographic stochasticity are not captured in our deterministic simulations, yet they are an important determinant of extinction risk, particularly for small populations (Lande, 1993). To incorporate the effects of interannual variation in environmental conditions (e.g., stream flows/temperatures) and the role of chance in the fate of small populations, we next implemented stochastic survival functions at multiple life stages to estimate average time to extinction of populations under different scenarios (Figure 1). Survival was partitioned between mature and immature animals to separately model fluctuations in recruitment success and sporadic harvest of breeding adults. For each year of the simulations, survival probabilities were randomly drawn from a uniform distribution of plausible values. We compared models where only the survival of immature individuals after emergence varied across years with models where survival of all individuals varied (Table 2, Figure 1b). For both survival scenarios, we explored the full range of nest failure rates (0%–100%) and variation in the number of available nest sites (0–30) to understand the interacting contributions of these processes. To account for uncertainty in the fate of larvae immediately following emergence from nests, we explored scenarios with varying strengths of density-dependent recruitment by modifying the β parameter (Table 2, Figure 1f). We ran 1000 simulations of each scenario and tallied the number of simulations that dropped below an arbitrary threshold (<5 adult females) over a 200-year projection. Dividing these tallies by 1000 gave the probability of quasi-extinction for each combination of nest site availability, nest failure rate, and adult mortality.

RESULTS

Deterministic simulations

We found that hellbender populations are predicted to persist under a broad range of nest fates (0%–80% failure)

when nest site availability and adult survival are both high (Figure 2), although the rate of nest failure determines the equilibrium abundance. Nest failure rates of 90% and 99%, however, result in population declines (Figure 2). We examined the population age structure over several time intervals for both the 90% and 99% nest failure scenarios (Figure 3); in both cases, the long-lived adults persisted for many years after the introduction of chronic recruitment failure, but populations dwindled toward a geriatric age structure over time (Figure 3). Unsurprisingly, when 99% of nests failed, it was catastrophic in all scenarios; all populations went extinct within 30 years. Although similar declines in population abundance occurred at 90% nest failure, populations persisted for over a century before complete collapse.

Removing the density-dependent terms in the model did not change our general conclusions (Appendix S1: Sections S1 and S2). Even without density-dependent larval emergence and survival, a tipping point still exists (at ~90% nest failure) where populations are no longer self-sustaining. Further, the speed of the decline when nest failure is increased beyond this threshold is comparable in simulations with and without density dependence. However, when density dependence is not accounted for, models yield population size estimates that are unrealistic (up to 2500 adults in a 1-km stretch of stream with only 30 nests). These unrealistic estimates reinforce our conclusion that density-dependent processes—such as competition for structural habitat shelter in silted streams—are likely limiting juvenile

survival in hellbender populations. Further, this finding highlights the importance of including density-dependent processes more generally; failure to account for density dependence can result in the tendency to overstate declines relative to historic abundances and generate overly optimistic forecasts regarding the rate of population recovery.

Stochastic simulations

Nest site availability, rates of nest failure, and the strength of density-dependent recruitment (juvenile survival) all exhibited a threshold beyond which extinction was certain (Figure 4). In most instances, stochastic adult survival increased extinction probability relative to the equivalent deterministic scenario and ultimately reduced the range of conditions under which populations were able to persist. Unsurprisingly, extinction probabilities increased with increasing rates of nest failure in a similar fashion to the deterministic simulations but exhibited a lower threshold beyond which extinction became inevitable (~80% vs. 90% failure; Figures 2 and 4). However, this robustness to extinction only held when nest availability was high; with fewer nests overall, extinction was inevitable at lower nest failure rates (~40%; Figure 4, Appendix S1: Section S3). In other words, when nest failure rates were high, the limited availability of nest sites (<10 nest sites available) was an important contributor to extinction risk (Figure 4a,b); however, the threat posed

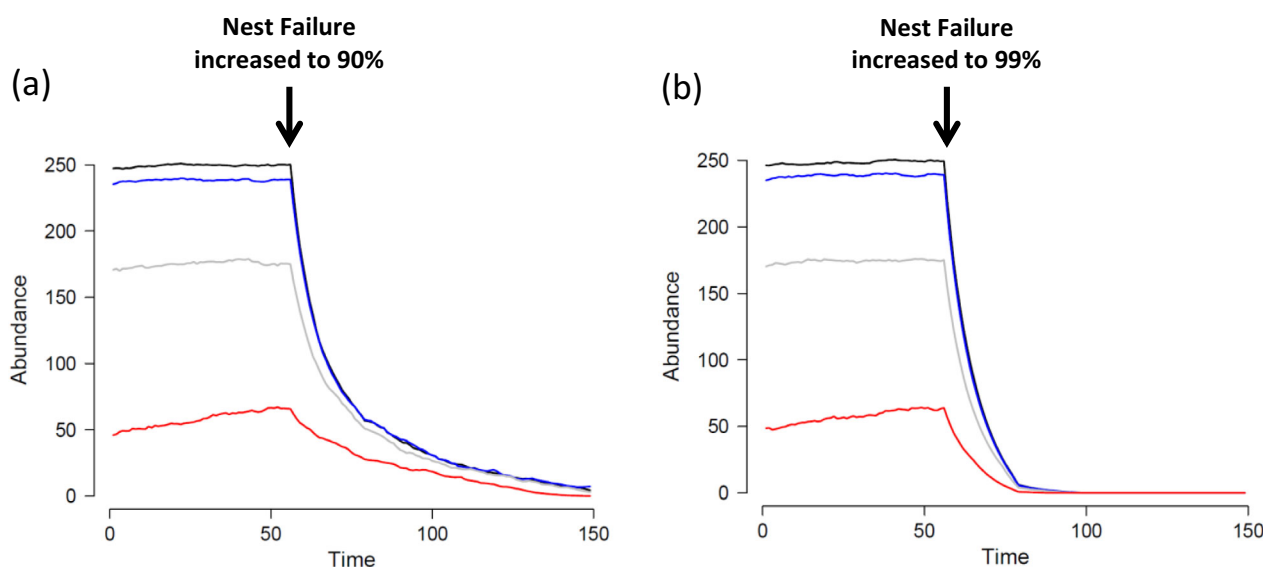


FIGURE 2 Projected abundance of adult hellbenders for various levels of nest failure (black line = 0% nest failure, blue line = 10% nest failure, gray line = 50% nest failure, red line = 80% nest failure), without nest site limitation. At 50 years, nest failure is increased to (a) 90% and (b) 99% for all scenarios to illustrate how populations respond to a shift in environmental conditions (e.g., deforestation of riparian buffers upstream of a population).

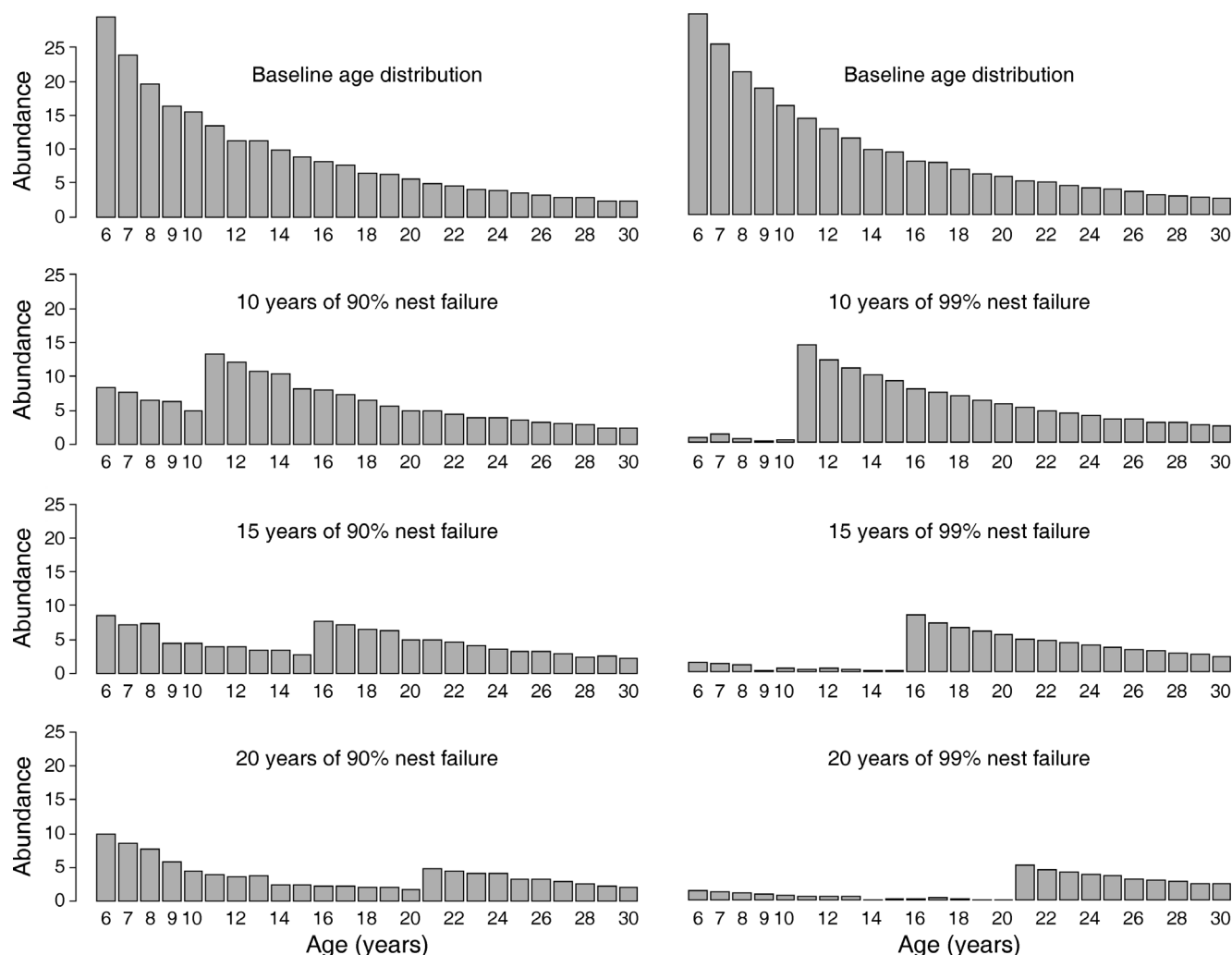


FIGURE 3 Change in adult age distribution following sharp decline in nest success. Top row represents stable age distribution at 50% nest failure (gray line in Figure 2). The subsequent panels illustrate the age distribution 10, 15, and 20 years after a shift to 90% (left column) and 99% (right column) nest failure. Immature individuals were excluded from the figure to make it easier to visualize declines of breeding adults.

by limited nest site availability was negligible if nest success was high. Extinction risk also increased as the strength of density-dependent recruitment increased, with a tipping point occurring at moderate levels of density dependence (Figure 4c,d). Similarly, our analysis showed that the effect of stochastic adult mortality was most severe when most nests failed and substantially increased the probability of extinction within 200 years (Figure 4a,b). Sensitivity analysis confirmed that variable adult survival exerted a greater effect on extinction risk than the specific form of the survival function (Appendix S1: Section S4). Increased nest site availability mitigated extinction risk only to a minor extent, suggesting the longevity of adults is more important for offsetting heavy juvenile losses in such scenarios. In summary, high rates of nest failure and/or juvenile mortality can lead to population collapse in our models. The

situation is most severe when adult mortality is high or, to a lesser extent, when nest sites are limited, because these act to critically undermine the population's ability to buffer against natural variation in recruitment.

DISCUSSION

Here we present a demographic model that incorporates key aspects of life history, particularly reproductive ecology and recruitment, to understand the population dynamics of a long-lived, highly fecund vertebrate. Our framework illustrates how multiple co-occurring threats impacting different stages of an organism's life cycle can undermine population viability and shows how the life history of hellbenders makes them particularly susceptible to extinction debt. We demonstrated that the high

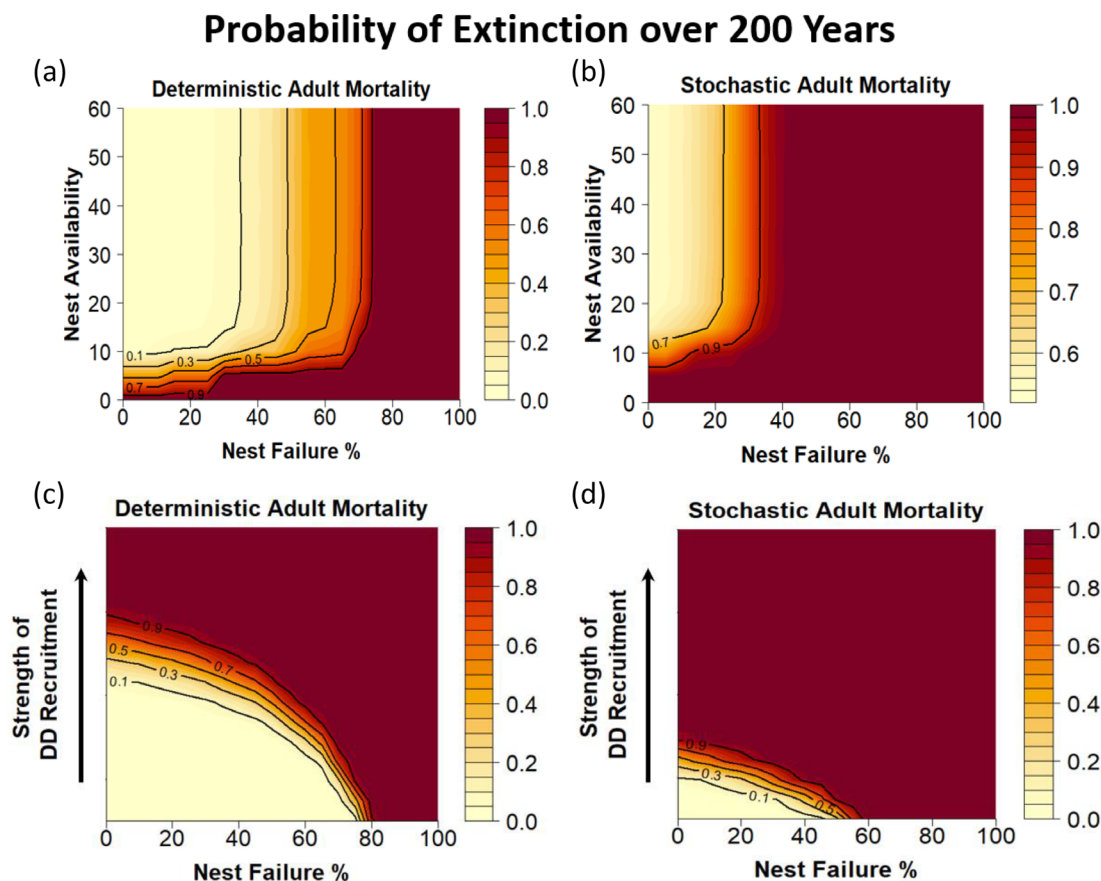


FIGURE 4 Extinction probabilities as a function of nest site availability, rate of nest failure, and strength of density-dependent (DD) recruitment. Extinction probabilities were obtained from 10,000 simulations projected over 200 years for each combination of factors. Darker shades indicate higher probabilities of extinction. Every scenario was simulated twice under deterministic (a, c) and stochastic (b, d) adult mortality. For scenarios exploring a range of nest site availabilities (a, b), uncertainty in the strength of density-dependent larval recruitment from year to year was captured by averaging extinction probabilities across scenarios, representing stochastic recruitment. For scenarios that explored a range of density-dependent recruitment levels (c, d), nest site availability was held constant at 30 nests.

rates of nest failure that have been observed in the field (Hopkins et al., 2023) are sufficient to drive hellbender populations toward a geriatric age distribution and eventually to localized extinction but that this process takes decades due to the species' longevity. As a result, population declines can go unnoticed for years because adults persist on the landscape. As has been shown in other long-lived taxa (Hutchings et al., 2012; Spencer et al., 2017), we also demonstrated that moderate reductions in the survival rates of mature hellbenders could threaten population persistence. In contrast, limited nest site availability alone had comparatively little influence on population dynamics due to density-dependent compensation in the juvenile stages, but limited nest sites can exacerbate the effects of excessive adult mortality and high rates of nest failure, quickly jeopardizing population viability.

Environmental stochasticity has led to the evolution of life histories that can overcome times of low productivity (Lande, 1993; Shaffer, 1981, 1987; Stearns, 1992); long-lived, highly fecund species are relatively robust to

annual variability in recruitment, and it is only typically chronic reproductive failure that will result in extinction debt and population declines (Hutchings et al., 2012). In contrast, however, long-lived, highly fecund species are sensitive to annual variability in adult mortality (Spencer et al., 2017). Population growth can be sensitive to changes in adult survival rates in long-lived species, such that any novel sources of adult mortality can quickly threaten the long-term persistence of populations (Biek et al., 2002; Congdon et al., 1994; Hels & Nachman, 2002; Kindsvater et al., 2016; Schmidt et al., 2005; Taylor & Scott, 1997; Vonesh & De la Cruz, 2002). For long lifespans to evolve, adult survival must be largely predictable (Stearns, 1992), and as such it is likely that survival rates of adult hellbenders remained relatively constant for much of their evolutionary history. In the contemporary era, however, novel sources of anthropogenic mortality emerged that can undermine the breeding population's ability to replace itself. Thus, quantifying the effect of stochasticity, in terms of which life stages it

influences and its impact on population growth, is essential to understand its contribution to extinction risk. Stochastic forces disproportionately threaten small populations (Lande, 1993), highlighting its importance in conservation fields. As demonstrated in our simulations, annual variability in adult survival rates acts to substantially increase extinction risk. Here we show that failing to account for stochastic forces results in overestimating the persistence probabilities of hellbenders (Figure 4), and this likely represents a common feature of population assessments for long-lived species with slow recovery times.

Long-lived species with high adult survival have evolved to persist with relatively low recruitment, where most juveniles do not survive to adulthood (Chesson & Warner, 1981; Childs et al., 2010; Warner & Chesson, 1985). As a result, the longevity of breeding adults can offset high juvenile mortality and enable population persistence, but our models show this may not be enough to prevent extinction in modified landscapes. First, even though hellbenders evolved to tolerate high rates of egg and larval mortality, there are limits above which populations will decline, especially when coupled with other threats operating on different life stages. Second, the combined effects of limited nest sites and elevated rates of nest failure create a scenario of extinction debt, in which local extirpation of hellbender populations becomes likely even when adults persist on the landscape. Any one of these factors alone can, to some extent, be compensated for by longevity, coupled with multiple bouts of reproduction, but taken together they undermine a population's ability to persist in landscapes impacted by humans. Unfortunately, knowledge concerning adult mortality is often lacking for long-lived species because the long-term studies required to obtain accurate estimates of survival rates are rare (Congdon et al., 1994). Demographic models can explore a range of scenarios in the face of such uncertainty but could be greatly improved with empirical data.

Assessments of population status require a comprehensive understanding of focal species' natural history. Future studies should seek to obtain missing pieces of natural history information that may strongly influence the dynamics of declining populations. Indeed, parameterizing our hellbender models has only become possible with the recent acquisition of data on key aspects of their reproductive ecology from nest box studies (Hopkins et al., 2023). These new insights have shed considerable light on the dynamics of early life stages, the factors that govern nest outcomes, and potential causes for recent declines. There are, however, several additional aspects of breeding behavior that we have omitted due to lack of detailed evidence: (1) multiple females depositing clutches at the same nest site (which may be particularly

important when nest sites are limiting), (2) competition for mates and/or nest sites (which may be size-based and reflect variation in the quality of nest sites), and (3) spatially explicit breeding dynamics. Similarly, the factors regulating larval and juvenile survival after emergence are largely unknown for many species, including hellbenders (Chan et al., 2018). As illustrated by our models, population dynamics of long-lived, highly fecund species are influenced strongly by our assumptions regarding density-dependent regulation. The strength of density-dependent survival in early life stages will determine the relative contribution of high fecundity to population resilience and, thus, control the tipping points that lead to declines (de Silva & Leimgruber, 2019; Reynolds et al., 2005). For hellbenders, increased siltation has been proposed as a mechanism that reduces the availability of habitat for newly emerged larvae (USFWS, 2018) and thereby strengthens the density-dependent mortality of early life stages. This idea, however, has yet to be formally tested. Improved techniques for detecting hellbender larvae would enable fundamental studies of larval ecology, which remains among the most important knowledge gaps for the species (Bodinof et al., 2012; Unger & Mathis, 2013). Studies specifically designed to quantify density dependence across life stages, and how they are affected by environmental change, would greatly advance our fundamental understanding of population regulation in hellbenders and other species of conservation concern.

Demographic models such as the one presented here can help to alleviate some of the challenges associated with population assessments of long-lived, highly fecund species (Beissinger & McCullough, 2002). By explicitly incorporating multiple stage-specific impacts into modeling frameworks, it is possible to gain insight into the contributions of different anthropogenic threats to the extinction risk of threatened and endangered taxa. This information can then be used to diagnose cryptic declines, identify instances of extinction debt, and outline the management interventions necessary for population recovery. Despite a long history of practitioners advocating for conservation that considers all life-history stages (Congdon et al., 1994; Mace et al., 2018; Wake & Vredenburg, 2008), there are still comparatively few studies that seek to quantify the combined impact of multiple, concurrent threats on the fate of wild populations. As we face unprecedented rates of environmental change, such a holistic approach will be necessary to preserve long-lived species that are disappearing throughout their range.

AUTHOR CONTRIBUTIONS

All authors conceived the ideas and designed the methodology. GCB and HKK performed the analysis. GCB led

the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code (Brooks et al., 2023) is available from Zenodo at <https://doi.org/10.5281/zenodo.10302585>.

ORCID

George C. Brooks  <https://orcid.org/0000-0001-9006-6465>

REFERENCES

- Alford, R. A., and S. J. Richards. 1999. "Global Amphibian Declines: A Problem in Applied Ecology." *Annual Review of Ecology and Systematics* 30: 133–165. <https://doi.org/10.1146/annurev.ecolsys.30.1.133>.
- Anderson, S. C., T. A. Branch, A. B. Cooper, and N. K. Dulvy. 2017. "Black-Swan Events in Animal Populations." *Proceedings of the National Academy of Sciences* 114: 3252–57. <https://doi.org/10.1073/pnas.1611525114>.
- Beissinger, S. R., and D. R. McCullough. 2002. *Population Viability Analysis*. Chicago: University of Chicago Press.
- Biek, R., W. C. Funk, B. A. Maxell, and L. S. Mills. 2002. "What Is Missing in Amphibian Decline Research: Insights from Ecological Sensitivity Analysis." *Conservation Biology* 16: 728–734. <https://doi.org/10.1046/j.1523-1739.2002.00433.x>.
- Bodinof, C. M., J. T. Briggler, R. E. Junge, T. Mong, J. Beringer, M. D. Wanner, C. D. Schuette, J. Ettling, and J. J. Millsbaugh. 2012. "Survival and Body Condition of Captive-Reared Juvenile Ozark Hellbenders (*Cryptobranchus alleganiensis bishopi*) Following Translocation to the Wild." *Copeia* 1: 150–59. <https://doi.org/10.1643/CH-11-024>.
- Bolten, A. B., L. B. Crowder, M. G. Dodd, S. L. MacPherson, J. A. Musick, B. A. Schroeder, B. E. Witherington, K. J. Long, and M. L. Snover. 2011. "Quantifying Multiple Threats to Endangered Species: An Example from Loggerhead Sea Turtles." *Frontiers in Ecology and the Environment* 9: 295–301. <https://doi.org/10.1890/090126>.
- Brooks, G. C., W. A. Hopkins, and H. K. Kindsvater. 2023. "Code for: Concurrent Threats and Extinction Risk in a Long-Lived, Highly Fecund Vertebrate with Parental Care." Zenodo, Dataset. <https://doi.org/10.5281/zenodo.10302585>.
- Brooks, G. C., and H. K. Kindsvater. 2022. "Early Development Drives Variation in Amphibian Vulnerability to Global Change." *Frontiers in Ecology and Evolution* 10: 813414. <https://doi.org/10.3389/fevo.2022.813414>.
- Browne, R. K., H. Li, Z. Wang, S. Okada, P. M. Hime, A. McMillan, M. Wu, R. Diaz, D. McGinnity, and J. T. Briggler. 2014. "The Giant Salamanders (Cryptobranchidae): Part B. Biogeography, Ecology and Reproduction." *Amphibian and Reptile Conservation* 5: 30–50.
- Burgmeier, N. G., S. D. Unger, T. M. Sutton, and R. N. Williams. 2011. "Population Status of Eastern Hellbender (*Cryptobranchus alleganiensis alleganiensis*) in Indiana." *Journal of Herpetology* 45: 195–201. <https://doi.org/10.1670/10-094.1>.
- Chan, K. Y. K., M. A. Sewell, and M. Byrne. 2018. "Revisiting the Larval Dispersal Black Box in the Anthropocene." *ICES Journal of Marine Science* 75: 1841–48. <https://doi.org/10.1093/icesjms/fsy097>.
- Chesson, P. L. 1984. "The Storage Effect in Stochastic Population Models." In *Mathematical Ecology* 76–89. Berlin: Springer.
- Chesson, P. L., and R. R. Warner. 1981. "Environmental Variability Promotes Coexistence in Lottery Competitive Systems." *The American Naturalist* 117: 923–943. <https://doi.org/10.1086/283778>.
- Childs, D. Z., C. J. E. Metcalf, and M. Rees. 2010. "Evolutionary Bet-Hedging in the Real World: Empirical Evidence and Challenges Revealed by Plants." *Proceedings of the Royal Society B: Biological Sciences* 277: 3055–64. <https://doi.org/10.1098/rspb.2010.0707>.
- Congdon, J. D., A. E. Dunham, and R. V. L. Sels. 1994. "Demographics of Common Snapping Turtles (*Chelydra serpentina*): Implications for Conservation and Management of Long-Lived Organisms." *American Zoologist* 34: 397–408. <https://doi.org/10.1093/icb/34.3.397>.
- Cox, N., B. E. Young, P. Bowles, M. Fernandez, J. Marin, G. Rapacciuolo, M. Böhm, et al. 2022. "A Global Reptile Assessment Highlights Shared Conservation Needs of Tetrapods." *Nature* 605: 285–290. <https://doi.org/10.1038/s41586-022-04664-7>.
- Crawford, B. A., J. C. Maerz, V. C. Terrell, and C. T. Moore. 2022. "Population Viability Analysis for a Pond-Breeding Amphibian Under Future Drought Scenarios in the Southeastern United States." *Global Ecology and Conservation* 36: e02119. <https://doi.org/10.1016/j.gecco.2022.e02119>.
- Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. "A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation." *Ecology* 68: 1412–23. <https://doi.org/10.2307/1939225>.
- de Silva, S., and P. Leimgruber. 2019. "Demographic Tipping Points as Early Indicators of Vulnerability for Slow-Breeding Megafaunal Populations." *Frontiers in Ecology and Evolution* 7: 171. <https://doi.org/10.3389/fevo.2019.00171>.
- d'Eon-Eggertson, F., N. K. Dulvy, and R. M. Peterman. 2015. "Reliable Identification of Declining Populations in an Uncertain

- World." *Conservation Letters* 8: 86–96. <https://doi.org/10.1111/conl.12123>.
- Donlan, C. J., D. K. Wingfield, L. B. Crowder, and C. Wilcox. 2010. "Using Expert Opinion Surveys to Rank Threats to Endangered Species: A Case Study with Sea Turtles." *Conservation Biology* 24: 1586–95. <https://doi.org/10.1111/j.1523-1739.2010.01541.x>.
- Foster, R. L., A. M. McMillan, and K. J. Roblee. 2009. "Population Status of Hellbender Salamanders (*Cryptobranchus alleganiensis*) in the Allegheny River Drainage of New York State." *Journal of Herpetology* 43: 579–588. <https://doi.org/10.1670/08-156.1>.
- Greenville, A. C., T. M. Newsome, G. M. Wardle, C. R. Dickman, W. J. Ripple, and B. R. Murray. 2021. "Simultaneously Operating Threats cannot Predict Extinction Risk." *Conservation Letters* 14: e12758. <https://doi.org/10.1111/conl.12758>.
- Hels, T., and G. Nachman. 2002. "Simulating Viability of a Spadefoot Toad *Pelobates fuscus* Metapopulation in a Landscape Fragmented by a Road." *Ecography* 25: 730–744. <https://doi.org/10.1034/j.1600-0587.2002.250609.x>.
- Hillis, R. E., and E. D. Bellis. 1971. "Some Aspects of the Ecology of the Hellbender, *Cryptobranchus alleganiensis alleganiensis*, in a Pennsylvania Stream." *Journal of Herpetology* 5: 121–26. <https://doi.org/10.2307/1562734>.
- Hopkins, W. A., B. F. Case, J. Groffen, G. C. Brooks, C. M. Bodinof Jachowski, S. T. Button, J. J. Hallagan, R. S. O'Brien, and H. K. Kindsvater. 2023. "Filial Cannibalism Leads to Chronic Nest Failure of Eastern Hellbender Salamanders (*Cryptobranchus alleganiensis*)." *The American Naturalist* 202: 92–106. <https://doi.org/10.1086/724819>.
- Humphries, W. J., and T. K. Pauley. 2005. "Life History of the Hellbender, *Cryptobranchus alleganiensis*, in a West Virginia Stream." *American Midland Naturalist* 154: 135–142. [https://doi.org/10.1674/0003-0031\(2005\)154\[0135:LHOTH2\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2005)154[0135:LHOTH2]2.0.CO;2).
- Hutchings, J. A., R. A. Myers, V. B. García, L. O. Lucifora, and A. Kuparinen. 2012. "Life-History Correlates of Extinction Risk and Recovery Potential." *Ecological Applications* 22: 1061–67. <https://doi.org/10.1890/11-1313.1>.
- Isaac, N. J., and G. Cowlshaw. 2004. "How Species Respond to Multiple Extinction Threats. Proceedings of the Royal Society of London." *Series B: Biological Sciences* 271: 1135–41. <https://doi.org/10.1098/rspb.2004.2724>.
- Jachowski, C. M. B., and W. A. Hopkins. 2018. "Loss of Catchment-Wide Riparian Forest Cover Is Associated with Reduced Recruitment in a Long-Lived Amphibian." *Biological Conservation* 220: 215–227. <https://doi.org/10.1016/j.biocon.2018.02.012>.
- Kimmel, K., M. Clark, and D. Tilman. 2022. "Impact of Multiple Small and Persistent Threats on Extinction Risk." *Conservation Biology* 36: e13901. <https://doi.org/10.1111/cobi.13901>.
- Kindsvater, H. K., K. T. Halvorsen, T. K. Sordalen, and S. H. Alonzo. 2020. "The Consequences of Size-Selective Fishing Mortality for Larval Production and Sustainable Yield in Species with Obligate Male Care." *Fish and Fisheries* 21: 1135–49. <https://doi.org/10.1111/faf.12491>.
- Kindsvater, H. K., M. Mangel, J. D. Reynolds, and N. K. Dulvy. 2016. "Ten Principles from Evolutionary Ecology Essential for Effective Marine Conservation." *Ecology and Evolution* 6: 2125–38. <https://doi.org/10.1002/ece3.2012>.
- Klug, H., and M. B. Bonsall. 2007. "When to Care for, Abandon, or Eat your Offspring: The Evolution of Parental Care and Filial Cannibalism." *The American Naturalist* 170: 886–901. <https://doi.org/10.1086/522936>.
- Klug, H., K. Lindstrom, and C. M. St. Mary. 2006. "Parents Benefit from Eating Offspring: Density-Dependent Egg Survivorship Compensates for Filial Cannibalism." *Evolution* 60: 2087–95. <https://doi.org/10.1554/05-283.1>.
- Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, et al. 2009. "Extinction Debt: A Challenge for Biodiversity Conservation." *Trends in Ecology and Evolution* 24: 564–571. <https://doi.org/10.1016/j.tree.2009.04.011>.
- Lande, R. 1993. "Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes." *The American Naturalist* 142: 911–927. <https://doi.org/10.1086/285580>.
- Mace, G. M., M. Barrett, N. D. Burgess, S. E. Cornell, R. Freeman, M. Grooten, and A. Purvis. 2018. "Aiming Higher to Bend the Curve of Biodiversity Loss." *Nature Sustainability* 1: 448–451. <https://doi.org/10.1038/s41893-018-0130-0>.
- Makowsky, R., L. A. Wilson, and T. K. Pauley. 2010. "Sexual Dimorphism in the Eastern Hellbender (*Cryptobranchus alleganiensis alleganiensis*)." *Herpetological Conservation and Biology* 5: 44–48.
- Mangel, M. 2006. *The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology*. Cambridge: Cambridge University Press.
- Manica, A. 2002. "Filial Cannibalism in Teleost Fish." *Biological Reviews* 77: 261–277. <https://doi.org/10.1017/S1464793101005905>.
- McRae, L., S. Deinet, and R. Freeman. 2017. "The Diversity-Weighted Living Planet Index: Controlling for Taxonomic Bias in a Global Biodiversity Indicator." *PLoS One* 12: e0169156. <https://doi.org/10.1371/journal.pone.0169156>.
- Nickerson, M. A., and J. T. Briggler. 2007. "Harvesting as a Factor in Population Decline of a Long-Lived Salamander; the Ozark Hellbender, *Cryptobranchus alleganiensis bishopi*." *Applied Herpetology* 4: 207–216. <https://doi.org/10.1163/157075407781268354>.
- Nickerson, M. A., and C. E. Mays. 1973. "A Study of the Ozark Hellbender *Cryptobranchus alleganiensis bishopi*." *Ecology* 54: 1164–65. <https://doi.org/10.2307/1935586>.
- Olson, Z. H., N. G. Burgmeier, P. A. Zollner, and R. N. Williams. 2013. "Survival Estimates for Adult Eastern Hellbenders and their Utility for Conservation." *Journal of Herpetology* 47: 71–74. <https://doi.org/10.1670/11-236>.
- Ono, K., Ø. Langangen, and N. C. Stenseth. 2019. "Improving Risk Assessments in Conservation Ecology." *Nature Communications* 10: 28–36. <https://doi.org/10.1038/s41467-019-10700-4>.
- Pechmann, J. H., and H. M. Wilbur. 1994. "Putting Declining Amphibian Populations in Perspective: Natural Fluctuations and Human Impacts." *Herpetologica* 50: 65–84.
- Peterson, C. L., D. E. Metter, B. T. Miller, R. F. Wilkinson, and M. S. Topping. 1988. "Demography of the Hellbender *Cryptobranchus alleganiensis* in the Ozarks." *American Midland Naturalist* 119: 291–303. <https://doi.org/10.2307/2425812>.
- Peterson, C. L., M. S. Topping, R. F. Wilkinson, Jr., and C. A. Taber. 1985. "Examination of Long-Term Growth of *Cryptobranchus alleganiensis* Predicted by Linear Regression Methods." *Copeia* 2: 492–96. <https://doi.org/10.2307/1444864>.

- Peterson, C. L., R. F. Wilkinson, Jr., M. S. Topping, and D. E. Metter. 1983. "Age and Growth of the Ozark Hellbender (*Cryptobranchus alleganiensis bishopi*)." *Copeia* 1: 225–231. <https://doi.org/10.2307/1444718>.
- Petranka, J. W. 1998. *Salamanders of the United States and Canada*. Washington DC: Smithsonian Institution Press.
- R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing <https://www.R-project.org/>.
- Reynolds, J. D. 2003. "Life Histories and Extinction Risk." In *Macroecology* 195–217. Oxford: Blackwell Publishing.
- Reynolds, J. D., N. K. Dulvy, N. B. Goodwin, and J. A. Hutchings. 2005. "Biology of Extinction Risk in Marine Fishes." *Proceedings of the Royal Society B: Biological Sciences* 272: 2337–44. <https://doi.org/10.1098/rspb.2005.3281>.
- Schmidt, B. R., R. Feldmann, and M. Schaub. 2005. "Demographic Processes Underlying Population Growth and Decline in *Salamandra salamandra*." *Conservation Biology* 19: 1149–56. <https://doi.org/10.1111/j.1523-1739.2005.00164.x>.
- Shaffer, M. L. 1981. "Minimum Population Sizes for Species Conservation." *Bioscience* 31: 131–34. <https://doi.org/10.2307/1308256>.
- Shaffer, M. L. 1987. "Minimum Viable Populations: Coping with Uncertainty." In *Viable Populations for Conservation*, edited by M. E. Soule, 69–86. New York: Cambridge University Press.
- Smith, B. G. 1907. "The Life History and Habits of *Cryptobranchus alleganiensis*." *Biological Bulletin* 13: 5–39.
- Spencer, R. J., J. U. Van Dyke, and M. B. Thompson. 2017. "Critically Evaluating Best Management Practices for Preventing Freshwater Turtle Extinctions." *Conservation Biology* 31: 1340–49. <https://doi.org/10.1111/cobi.12930>.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Taber, C. A., R. F. Wilkinson, Jr., and M. S. Topping. 1975. "Age and Growth of Hellbenders in the Niangua River, Missouri." *Copeia* 4: 633–39. <https://doi.org/10.2307/1443315>.
- Taylor, B. E., and D. E. Scott. 1997. "Effects of Larval Density Dependence on Population Dynamics of *Ambystoma Opacum*." *Herpetologica* 53: 132–145.
- Taylor, B. E., D. E. Scott, and J. W. Gibbons. 2006. "Catastrophic Reproductive Failure, Terrestrial Survival, and Persistence of the Marbled Salamander." *Conservation Biology* 20: 792–801. <https://doi.org/10.1111/j.1523-1739.2005.00321.x>.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. "Habitat Destruction and the Extinction Debt." *Nature* 371: 65–66. <https://doi.org/10.1038/371065a0>.
- Todd, B. D., S. M. Blomquist, E. B. Harper, and M. S. Osbourn. 2014. "Effects of Timber Harvesting on Terrestrial Survival of Pond-Breeding Amphibians." *Forest Ecology and Management* 313: 123–131. <https://doi.org/10.1016/j.foreco.2013.11.011>.
- Topping, M. S., and C. A. Ingersol. 1981. "Fecundity in the Hellbender, *Cryptobranchus Alleganiensis*." *Copeia* 4: 873–76. <https://doi.org/10.2307/1444188>.
- Unger, S. D., and A. Mathis. 2013. "Larval Growth and the Potential for Head-Starting of Eastern and Ozark Hellbenders (*Cryptobranchus alleganiensis alleganiensis* and *C. a. Bishopi*)." *Herpetological Review* 44: 89–91.
- Unger, S. D., T. M. Sutton, and R. N. Williams. 2013. "Projected Population Persistence of Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) Using a Stage-Structured Life-History Model and Population Viability Analysis." *Journal for Nature Conservation* 21: 423–432. <https://doi.org/10.1016/j.jnc.2013.06.002>.
- USFWS (US Fish and Wildlife Service). 2018. *Species Status Assessment Report for the Eastern Hellbender (Cryptobranchus alleganiensis)*. Washington, DC: USFWS.
- Vonesh, J. R., and O. De la Cruz. 2002. "Complex Life Cycles and Density Dependence: Assessing the Contribution of Egg Mortality to Amphibian Declines." *Oecologia* 133: 325–333. <https://doi.org/10.1007/s00442-002-1039-9>.
- Wake, D. B., and V. T. Vredenburg. 2008. "Are we in the Midst of the Sixth Mass Extinction? A View from the World of Amphibians." *Proceedings of the National Academy of Sciences* 105: 11466–73. <https://doi.org/10.1073/pnas.0801921105>.
- Warner, R. R., and P. L. Chesson. 1985. "Coexistence Mediated by Recruitment Fluctuations: A Field Guide to the Storage Effect." *The American Naturalist* 125: 769–787. <https://doi.org/10.1086/284379>.
- Wheeler, B. A., E. Prosen, A. Mathis, and R. F. Wilkinson. 2003. "Population Declines of a Long-Lived Salamander: A 20 + –Year Study of Hellbenders, *Cryptobranchus alleganiensis*." *Biological Conservation* 109: 151–56. [https://doi.org/10.1016/S0006-3207\(02\)00136-2](https://doi.org/10.1016/S0006-3207(02)00136-2).
- Wiggs, J. N. 1976. *Food Habits, Starvation and Growth in the Hellbender, Cryptobranchus Alleganiensis*. Master's Dissertation, Missouri State University, Springfield, MO.
- Wilbur, H. M. 1980. "Complex Life Cycles." *Annual Review of Ecology and Systematics* 11: 67–93. <https://doi.org/10.1146/annurev.es.11.110180.000435>.

SUPPORTING INFORMATION

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

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