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ORIGINAL ARTICLE

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Predicting the population viability of an endangered amphibian under environmental and demographic uncertainty

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Abstract

Population viability analyses (PVAs) represent a key component of many recovery plans for threatened and endangered species. Demography links the processes that affect individuals to population-level patterns, and hence projections constructed from demographic data are the most common tools for PVAs. We constructed a size-structured integral projection model (IPM) for the United States federally endangered Reticulated Flatwoods Salamander, *Ambystoma bishopi*, to evaluate demographic influences on population growth and predict the efficacy of future management actions. Flatwoods salamanders breed in ephemeral wetlands in the Southeastern United States. The ephemeral nature of breeding sites can result in complete recruitment failure in drought years when wetlands fail to fill, or dry before metamorphosis occurs. As a result, this species exhibits marked temporal variability in vital rates that must be accounted for in projection models. We constructed a stochastic IPM using 13 years of mark-recapture data (2010–2023) from two breeding wetlands. Variable survival rates exhibited by flatwoods salamanders, coupled with a high probability of recruitment failure, result in a low predicted probability of population persistence. Sensitivity analyses revealed age at maturity and the frequency of recruitment exerted the greatest influence on population growth, and thus managers should prioritize conservation efforts that target these demographic processes. Additional management should consider strategies to dampen temporal variability in larval survival, something that could be achieved through emergency salvage operations, captive rearing efforts, and manipulation of wetland hydroperiods.

KEYWORDS

Ambystoma bishopi, conservation, extinction, flatwoods salamander, integral projection model

1 | INTRODUCTION

Global amphibian declines represent a problem ideally suited for the practical application of population viability analyses (PVAs; Collins & Storfer, 2003; Halley et al., 1996; Wood et al., 2018). A large body of work indicates that all stages of the amphibian life cycle must be considered to understand trends in populations and vulnerability to anthropogenic threats (Biek et al., 2002; Harper et al., 2008; Hels & Nachman, 2002; Messerman et al., 2023; Taylor & Scott, 1997; Terrell et al., 2023; Vonesh & De la Cruz, 2002). Many previous studies attempting to diagnose amphibian declines limited their focus to a single vital rate (reviewed in Biek et al., 2002; Forbes & Calow, 2002; Schmidt et al., 2005; Vonesh & De la Cruz, 2002) or to individual-level effects (Boone & Bridges, 2003; Kiesecker et al., 2001; Schmidt et al., 2005), despite population growth being the quantity of interest (Forbes & Calow, 2002; Messerman et al., 2023; Schmidt et al., 2005; Terrell et al., 2023). As a result, disagreement still exists in the amphibian conservation community as to what constitutes effective management for imperiled species (Messerman et al., 2023, Terrell et al., 2023).

Population viability analysis (PVA) is a modeling framework that uses demographic data from individual species to evaluate extinction risk, causative agents of decline, and management strategies to promote future recovery (Akçakaya & Sjögren-Gulve, 2000; Bakker & Doak, 2009; Beissinger & McCullough, 2002). The field of PVAs emerged from the application of demographic modeling and population genetics to species declines (Soulé, 1987). PVAs are popular in conservation fields because they can account for uncertainty in population parameters, incorporate multiple, disparate data types, and often directly translate to management recommendations (Akçakaya & Sjögren-Gulve, 2000; Himes-Boor, 2014; Oppel et al., 2014). Further, PVAs provide a useful mechanism to compare alternative scenarios when empirical data is either deficient or impossible to obtain (Beissinger & McCullough, 2002; Brook et al., 2000; Platt, 1964; Van Poorten et al., 2019).

Here we construct an integral projection model (IPM) for the United States federally endangered Reticulated Flatwoods Salamander (*Ambystoma bishopi*, hereafter flatwoods salamander), and estimate extinction risk under demographic and environmental stochasticity. IPMs allow demographic vital rates to be governed by continuous traits, such as body size or weight (Ellner et al., 2016; Merow et al., 2014). IPMs have recently been used in several conservation projects and now present a flexible methodology for examining a variety of different population level processes across many taxa (Caruso et al., 2020; Lown et al., 2020; Schreiber & Ross, 2016). We chose an IPM framework to model flatwood salamander populations owing to the strong link between body size and vital rates (Brooks, 2020; Brooks et al., 2020; Brooks et al., in press; Chandler & Brooks, in press). IPMs can also readily account for species, like amphibians, with distinct life stages that exert contrasting effects on population growth (Messerman et al., 2023). Our model incorporates continuous relationships between body size and key demographic parameters (e.g., survival and fecundity) and accounts for individual growth through time (Childs et al., 2004; Coulson, 2012; Ellner et al., 2016; Merow et al., 2014). We perform a sensitivity analysis of the demographic model to identify components of the life history that exert the greatest influence on population growth. Our objectives were to (1) parameterize a population model using compiled demographic data, (2) evaluate the sensitivity of population growth to changes in vital rates, and (3) project populations to quantify extinction risk under different levels of survival and breeding frequency. We predict that adult survival will interact with the frequency of successful breeding to determine extinction risk. We also predict that, because of the relationship between body size and survival, size at metamorphosis will influence population growth rates. We highlight the implications of our results for flatwoods salamander recovery efforts and discuss our findings more broadly regarding the utility of demographic modeling for amphibian conservation.

2 | METHODS

2.1 | Study system

Flatwoods salamanders are native to Longleaf Pine (*Pinus palustris*) savannas in the southeastern United States. Adults are fossorial, residing in upland habitats for most of their lives, and undergo annual breeding migrations to ephemeral wetlands from October to December. Flatwoods salamanders migrate before wetlands fill and oviposit in dry wetland basins; because individual females scatter eggs rather than laying an egg mass, clutch size estimates have been challenging to obtain from field studies. Eggs hatch several weeks after laying following inundation (Anderson & Williamson, 1976; Brooks et al., 2019; Palis, 1997). Complete reproductive failure is common due to late wetland filling or premature wetland drying (Brooks, 2020; Brooks et al., 2019; Palis et al., 2006). Following metamorphosis, individuals disperse from natal wetlands into upland habitats and typically reach sexual maturity in 1 or 2 years (Brooks, 2020; Brooks et al., 2020; Palis, 1997). Adults live for up to 13 years in the wild, with an average lifespan of 5–7 years (Brooks et al., 2020, 2023). A life-cycle diagram with associated vital rates is presented in Figure 1.

We studied two flatwoods salamander populations on Eglin Air Force Base in Okaloosa County, Florida from 2010 to 2023 (13 breeding seasons). These two populations breed in two small pine flatwoods wetlands (Pond 4: 0.45 ha; Pond 5: 0.36 ha). We completely encircled each breeding wetland with an aluminum flashing drift fence and captured salamanders moving into and out of wetlands each breeding season. The dates that drift fences were operational changed through time in response to weather conditions and staff availability, but we generally attempted to open fences in time to capture the first movement of individuals in the fall (October–November). We typically ran fences into the spring only when metamorphosis was likely (identified through larval dipnet surveys conducted every January through April) due to suitable hydrologic conditions. We measured (snout–vent length [SVL]) and marked all captured metamorph and adult salamanders using a combination of Visual Implant Elastomers and Passive Integrated Transponder tags. Additional details of drift fencing methodologies are described in Erwin et al. (2016).

2.2 | Population model

We constructed an IPM to model the population dynamics of flatwoods salamanders and quantify extinction risk under different scenarios. Our modeling framework accounts for variation within a population based on some continuous individual trait (body size) by dividing individuals into sufficient discrete stages or age/size groups to approximate continuous functions (Easterling et al., 2000; Ellner et al., 2016; Rees et al., 2014).

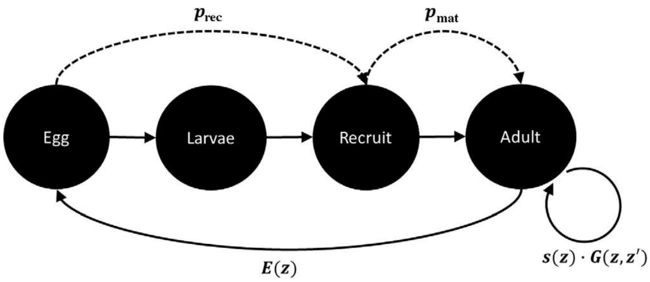

FIGURE 1 The Reticulated Flatwoods Salamander (*Ambystoma bishopi*) life cycle. Eggs are laid in dry wetland basins, and the number of eggs deposited by each female, $E(z)$, is positively related to body size, z. Larvae grow for several months before undergoing metamorphosis and recruit into the terrestrial population with probability p_{rec}. Individuals typically take 1 or 2 years to reach sexual maturity (p_{mat}). Once mature, adults continue to grow with probability $G(z,z')$ and experience annual, size-dependent survival rates $s(z)$.

For any point in time, the population size in an IPM framework at time $t+1$ is given by:

$$n(z',t+1)=\int_L^U \left(s(z)\cdot G(z',z)+F(z',z)\right)\cdot n(z,t)dz,$$

where z is a measure of body size, and $n(z,t)$ is the size distribution of the population at time t. The IPM contains several functions, known as kernels, that describe probabilistic transitions between size classes. $s(z)$ is a function describing the probability of survival based on size

$$s(z)=\mu+\beta z.$$

$G(z',z)$ (the growth kernel) is the probability that an individual grows from size z to z', estimated using a von Bertalanffy growth equation

$$z_{t+1}=z_t+(L_\infty-z_t)\left(1-e^{-k}\right),$$

and $F(z',z)$ (the fecundity kernel) is the probability of recruitment of size z' individuals based on the number and size of breeding females. The fecundity kernel describes fecundity based on female body size, such that

$$F(z',z)=p_{\text{mat}}\times E(z)\times p_{\text{rec}},$$

where p_{mat} represents the probability that females reproduce in a given year, $E(z)$ is the number of offspring produced by a female of size z, and p_{rec} is the probability that offspring survive and enter the breeding population. The size distribution of the new recruits (z') is assumed to be normally distributed and dependent on the wetland hydroperiod in a given year. The equation is integrated from L (the lower size limit) to U (the upper size limit). This range includes all possible body sizes that individuals can achieve, either by growth or shrinkage.

2.3 | Demographic functions

To parameterize the IPM, we used mark-recapture data collected from drift fences to build several functions describing important aspects of flatwoods salamander demography. Some of this work has been published elsewhere, but we briefly describe the essential demographic functions here. We assessed growth of post-metamorphic salamanders, $G(z,z')$, using the "growth increment" form of the von Bertalanffy model (Fabens, 1965), while accounting for individual-level variation in parameters

TABLE 1 Equations used to model the vital rates of Reticulated Flatwoods Salamanders (*Ambystoma bishopi*).

Description	Equation
von Bertalanffy growth equation	$z_{t+1} = z_t + (L_\infty - z_t)(1 - e^{-k})$
Annual survival probability	$s(z) = \mu + \beta z$
Size-dependent maturity	$p_{\text{mat}} = \frac{1}{1+e^{a+bz}}$
Egg production (Poisson)	$E(z) = c + mz$
Recruitment	$E(z) \times p_{\text{mat}} \times p_{\text{rec}}$

Note: Sources provided were used either in full or in part as justification for parameter values, and most parameters were directly estimated from 13 years of drift fence data monitoring two flatwoods salamander populations. Body size is represented by z, all other parameters are described in Table 2.

defining the growth function (Brooks et al., 2020). In the present analysis, we lowered the variance in growth of the largest individuals to reduce the frequency of eviction from the IPM (Williams et al., 2012). We modeled maturation and reproductive output (egg production) as a function of body size. We generated a logistic maturation curve based on the size of the smallest gravid female captured during the present study and developed clutch size—body size relationships using available data from the published literature (Anderson & Williamson, 1976) and by counting eggs in preserved specimens from the Georgia Southern University—Savannah Science Museum Herpetology Collection (Chandler & Brooks, in press). We used a generalized linear model with a Poisson error distribution to describe the relationship between female body size and number of eggs produced (Chandler & Brooks, in press). In addition to a fecundity model, we created two functions describing the body-size distribution of new individuals (metamorphs) recruited to the breeding population. Hydrologic variation has been shown to influence the size at metamorphosis in flatwoods salamanders (Brooks et al., 2020). To mimic this environmental variability, we created functions to model short and long hydroperiod breeding years, respectively. Short and long hydroperiods represent <15 weeks and >15 weeks of standing water, respectively, and result in a difference of approximately 10 mm in the average size of emerging metamorphs (Brooks et al., 2020). The size distribution of new recruits is assumed to be normally distributed (Brooks et al., 2020). The fecundity model combined with the size distribution of new recruits fully describes the fecundity kernel, $F(z,z')$. Following metamorphosis and recruitment to the terrestrial population, individuals survive at a rate proportional to their body size, $s(z)$ (Brooks et al., in press). Survival was estimated using a modified Cormack-Jolly–Seber model that can account for imperfect detection and incorporates body size as a continuous predictor variable (Brooks et al., in press). We report equations in Table 1 and parameter estimates and their associated variability for all demographic functions in Table 2 and Figure 2.

2.4 | Deterministic simulations

To examine the effects of different parameter values on population growth rate, we conducted elasticity and sensitivity analyses of both the survival-growth and fecundity kernels (Easterling et al., 2000). This process involves the manual perturbation of vital rates to quantify how changes in a small region of the survivorship/fecundity surfaces (Figure 2e,f) affect the dominant eigenvalue (Easterling et al., 2000). Additionally, to explore the consequences of parameter uncertainty in more detail, we constructed a set of models where certain parameters were held constant across model runs (Ellner & Rees, 2007). Specifically, we focused on the effects of different reproductive values on population growth rate, while holding survival constant across years. We fixed the percentage of female salamanders reproducing in each breeding season (50%, 75%, or 100%) and the probability of surviving from an egg to returning in the following year (1%, 2%, 3%, 4%, or 5%) and calculated long-term population growth rates for each scenario. Including different percentages of mature females breeding each year accounts for uncertainty in whether individuals skip breeding years, as has been shown for other pond-breeding amphibians (e.g., Cayuela et al., 2014), and the range of survival probabilities from egg to metamorph encapsulates the range of values we have observed in the field.

2.5 | Stochastic simulations

To quantify extinction risk under different life-history scenarios, we performed stochastic simulations under different life-history scenarios. For stochastic simulations, survival, maturation, growth, and fecundity parameter values were randomly drawn from Bayesian posterior distributions to account for parameter uncertainty (Ellner & Rees, 2007; Rees & Ellner, 2009). Paired parameter values for each function (e.g., slopes and intercepts) were selected from the same sample positions along the posteriors. Additionally, certain reproductive parameters were varied each year to simulate environmental variability. Specifically, for each year of the simulation, we randomly selected a proportion of eggs surviving to return in the following year (1%–5%) and a proportion of

TABLE 2 Life history parameters used to construct an Integral Projection Model describing the population dynamics of Reticulated Flatwoods Salamanders (*Ambystoma bishopi*).

Parameter description	Values	Source(s)
Asymptotic size (mm) in von Bertalanffy growth model (L_∞)	70.0–77.9	Brooks et al. (2020)
Growth coefficient in von Bertalanffy growth model (k)	0.16–0.47	Brooks et al. (2020)
Deviation in growth for individuals $<L_\infty$	3	Brooks et al. (2020)
Deviation in growth for individuals $>L_\infty$	1	-
Mortality rate scale coefficient (μ)	0.74–1.31	Brooks et al. (2020) and Brooks et al. (in press)
Mortality rate coefficient (β)	0.10–0.24	Brooks et al. (2020) and Brooks et al. (in press)
Slope of the size-dependent fecundity function (m)	8.53	Anderson and Williamson (1976) and Chandler and Brooks (in press)
Intercept of the size-dependent fecundity function (c)	−362.6	Anderson and Williamson (1976) and Chandler and Brooks (in press)
Slope of the maturity function (b)	1.5	Brooks et al. (2020) and Chandler (2023)
Intercept of the maturity function (a), drawn from a uniform distribution	65–75	Brooks et al. (2020) and Chandler (2023)
Probability of recruitment from egg to metamorph, drawn from a uniform distribution	0.01–0.05	Brooks et al. (2020), Shoop (1974), Petranka (1989), and Stangel (1988)
Mean metamorph size during long hydroperiod years, drawn from a uniform distribution	40.7–44.7	Brooks et al. (2020)
Deviation in metamorph size during long hydroperiod years	3.7	Brooks et al. (2020)
Mean metamorph size during short hydroperiod years, drawn from a uniform distribution	33.1–37.1	Brooks et al. (2020)
Deviation in metamorph size during short hydroperiod years	2.7	Brooks et al. (2020)

Note: Sources provided were used either in full or in part as justification for parameter values, and most parameters were directly estimated from 13 years of drift fence data monitoring two flatwoods salamander populations. The parameter for deviation in growth for individuals $>L_\infty$ was arbitrarily chosen to improve model fit (i.e., reduce eviction of large individuals, Williams et al., 2012).

females breeding (50%, 75%, or 100%). We set all models as female only models with an initial population size of 50 individuals. Initial population density was generated based on population densities observed in the wild. We set a ceiling of 100 (females) for all simulations based on observed population sizes for these sites. However, given the uncertainty in carrying capacity of terrestrial uplands surrounding breeding wetlands, and variability in population sizes across wetlands, we performed additional analyses with ceilings set to 50 and 200 females, respectively. Survival was assumed to be constant across years, but we repeated the stochastic simulations under the 10th and 90th percentile estimates for the survival function to characterize its effect (Figure 2). We also fixed the frequency of complete reproductive failure due to unsuitable hydrology at either 50%, 67%, or 75% to explore the effect of extreme drought conditions on long-term population viability. Across all simulations, populations were projected for 70 years, and we calculated extinction probability as the number of populations that declined below a quasi-extinction threshold of five individuals across 1000 replicate model runs. All analyses were conducted in R (R Core Team, 2023).

3 | RESULTS

We found that when assuming a constant kernel (deterministic simulations) using parameters from a successful breeding year, the long-term population growth rate (λ) was almost always greater than one (Figure 3). While holding post-metamorphic survival constant across years, there was a noticeable positive effect of longer hydroperiod (implemented through metamorph size) on population growth rate in successful breeding years (Figure 3). Specifically, scenarios with long hydroperiods (and therefore large metamorph body sizes) had population growth rates 5%–30% higher than scenarios with short hydroperiods. Changing the proportion of breeding females had a larger effect during years when a higher proportion of eggs reached metamorphosis (Figure 3). Specifically, when 5% of eggs survived to metamorphosis, scenarios in

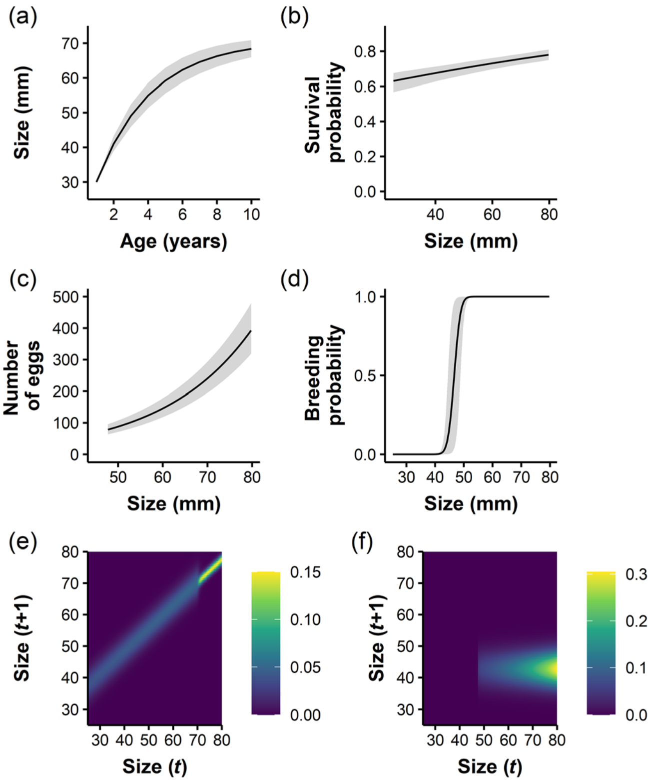

FIGURE 2 Demographic functions used to construct the kernels of an Integral Projection Model for Reticulated Flatwoods Salamanders (*Ambystoma bishopi*). Vital rates presented include (a) growth, described by a von Bertalanffy equation, (b) survival rate as a function of body size, (c) clutch size as a function of body size, and (d) maturation as a function of body size. As is typical for amphibians, body size is measured as snout–vent length (SVL). Also presented are the (e) survival-growth and (f) fecundity kernels produced from the vital rate functions that comprise the full IPM.

which all females bred each year had population growth rates 30% higher than scenarios in which half of females skipped breeding. In contrast, when 1% of eggs survived to metamorphosis, population growth rates only differed by 15% in the two scenarios. Furthermore, small increases in the proportion of eggs surviving through metamorphosis had large effects on population growth rate (e.g., increases in average λ ranging from 41% to 54% in long hydroperiod years), regardless of hydroperiod length or the proportion of females breeding. In the absence of recruitment, time to extinction averaged 5 years, but was strongly tied to our assumptions regarding adult survival (95% CI: 2–10 years).

Sensitivity and elasticity analyses for the fully stochastic kernel in years with long hydroperiods showed similar results. Kernel level sensitivity indicated that changes to the kernel impacting the growth of juveniles into the reproductive size classes had the largest impacts on population growth rate (Figure 4). Elasticity analyses indicated that population growth showed the biggest change in response to changes in survival and growth of individuals near the size at first reproduction. Additionally, changes to transitions of the most common sizes in the fecundity kernel strongly influenced population growth rates (Figure 4). The results were similar in years with short hydroperiods but were generally shifted towards the smaller-sized offspring in these years (Figure S1).

As expected, the frequency of successful breeding seasons had strong effects on extinction rates through time (Figure 5). For example, at median survival rates, increasing the average frequency of reproductive failure from 50% to 67% raised the extinction probability from approximately 8% to 59% after 70 years, and increasing the average frequency of reproductive failure from 67% to 75% raised the extinction probability from approximately 59%–95% after 70 years (Figure 5). Therefore, with all else being equal, successful recruitment is required on average every other year for these populations to have a high likelihood of persistence. Extinction risk also varied dramatically with different assumed survival rates (e.g., 10th percentile of adult survival = 16% extinction probability vs. 90th percentile of adult survival = 4% extinction probability with a 50% chance for reproduction to occur; Figure 5). Even though the magnitude of change is smaller compared to those brought about by changes in reproductive failure, we note that our uncertainty in survival rates reflects a ≥4-fold discrepancy in extinction probability. Further, lowering the maximum number of individuals had a strong effect on the number of years that a population was likely to persist, such that when the population ceiling was halved ($K = 50$), extinction probabilities approached one in all scenarios with a 25% chance of reproduction (Figure S2). Similarly, when the population ceiling was increased to 200 individuals, the extinction probability was at its lowest across all reproduction frequencies (Figure S3).

4 | DISCUSSION

We used a 13-year demographic dataset to build an IPM for flatwoods salamanders and assess extinction probability over a 70-year period under different scenarios. We found that although flatwoods salamanders appear to be able to rapidly recover from declines, a succession of years with recruitment failure coupled with low or variable survival can drive populations to extinction. Further, population growth was sensitive to size at metamorphosis and post-metamorphic, juvenile growth rates, suggesting that large metamorphs capable of maturing within a year are critical to population persistence.

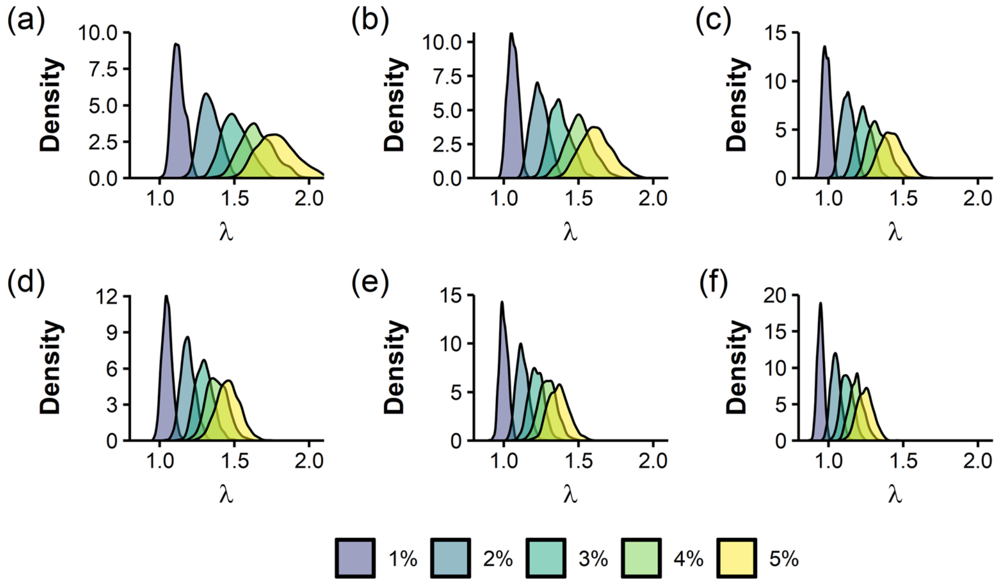

FIGURE 3 Population growth rates (λ) for various parameterizations of the fecundity kernel for an Integral Projection Model describing the population dynamics of Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) during successful breeding years. Fecundity kernels were parameterized with both large (a–c) or small (d–f) metamorph size distributions, reflecting differences in wetland conditions. The percentage of adult females returning to the wetland to breed ranged from 100% (a and d) to 75% (b and e) to 50% (c and f). Finally, the probability of individuals starting as eggs, surviving through metamorphosis, and returning to the wetland in the following year was 1%–5%. Post-metamorphic survival was held constant across years.

Across all model parameterizations, IPM results generally displayed fluctuating population sizes that are characteristic of amphibian species breeding in temporally dynamic ephemeral wetland systems (Crawford et al., 2022; Taylor et al., 2006). Even though there was substantial variability in potential parameterization of the fecundity kernel, population growth rates during successful breeding seasons were almost always greater than one and could approach two during exceptional years. Only two or three successful breeding years were needed to rapidly increase population size from small (<10 females) to near the carrying capacity. Carrying capacity is unknown in these systems, but increasing carrying capacity would allow this rapid increase to improve long-term persistence. An important management strategy could be managing and protecting suitable upland habitat with high availability of burrows and invertebrate prey in order to increase carrying capacity. Another potential management strategy may be to identify successive dry years that will put populations at risk of extinction, and focus captive rearing or larval headstarting efforts during that time (Griffiths & Pavajeau, 2008). Alternatively, the artificial manipulation of wetland hydroperiods (to achieve consistent recruitment) may offer a more cost-effective method to mitigate periodic droughts (Mathwin et al., 2021).

We found support for our prediction that adult survival interacts with the frequency of successful breeding to determine extinction risk. High adult survival was uniformly important across all scenarios in allowing populations to persist through years with reproductive failure (Biek et al., 2002; Griffiths et al., 2010; Kissel et al., 2020). One important limitation to the current modeling framework is a limited mechanistic knowledge of the factors impacting adult survival, although previous research has indicated that survival does vary annually (Brooks et al., in press). Other research suggests that adult amphibian survival is likely linked to weather conditions experienced post-metamorphosis (Cayuela et al., 2016; Messerman et al., 2023; Rittenhouse et al., 2009) as well as the availability of suitable cover and retreat sites (e.g., Rothermel & Luhring, 2005; Roznik & Reichling, 2021). Thus, it is an important research need to understand the mechanisms impacting adult survival in flatwoods salamanders (e.g., the relationship between upland habitat quality or climate and survival) and incorporate those relationships into future iterations of these population viability models.

We also found support for our prediction that size at metamorphosis influences population growth rates. The IPM framework used here allowed us to quantify the potential effects of differing hydroperiods on body size at metamorphosis. Brooks et al. (2020) found that flatwoods salamander metamorphs were, on average, smaller during years with shorter hydroperiods than years with longer hydroperiods, and this trend has also

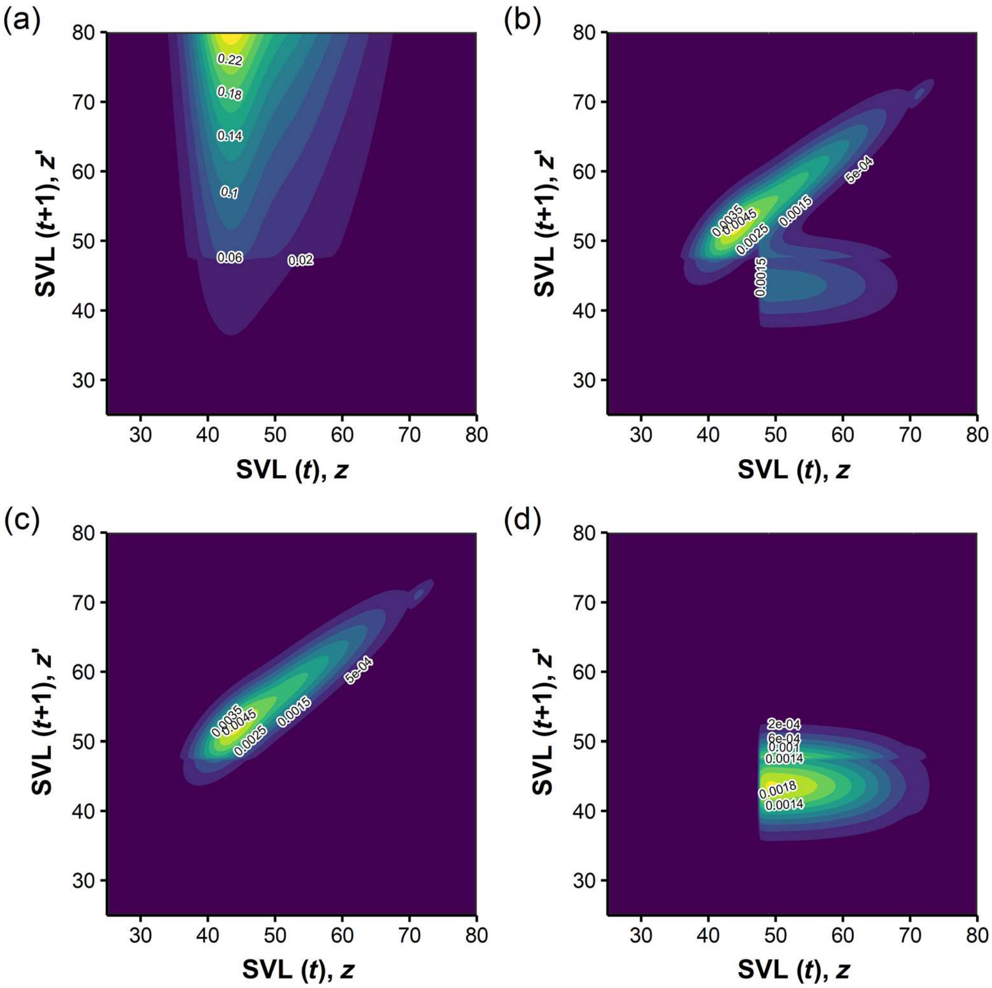

FIGURE 4 Sensitivity (a) and elasticity (b–d) analyses of the IPM kernels during years with successful recruitment. Elasticity is displayed for the complete IPM (b), in addition to the growth (c) and fecundity (d) kernels separately. Analyses were performed on years with long hydroperiods (e.g., years that yield large-bodied metamorphs). The average population growth rate (λ) of years with long hydroperiods was 1.5. As is typical for amphibians, body size (z) is measured as snout–vent length (SVL). The equivalent analysis for years with short hydroperiods (small metamorphs) is presented in the Supporting Information.

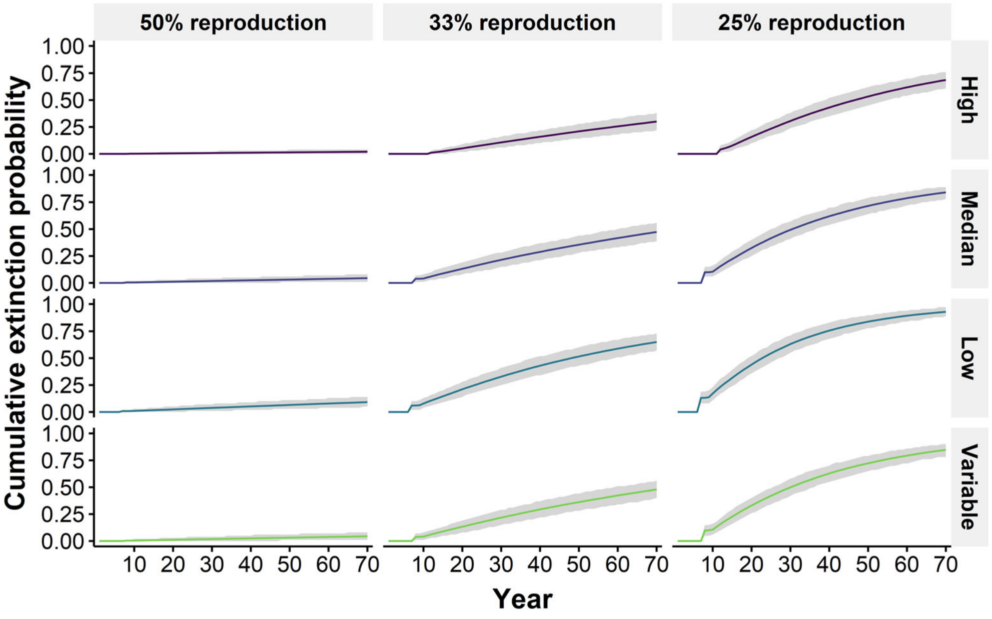

FIGURE 5 Extinction probabilities for Reticulated Flatwoods Salamander (*Ambystoma bishopi*) populations with a carrying capacity of 100 females. Probability of successful breeding ranges from 25% to 50%, and post-metamorphic survival was held constant at the 90th (high), 50th (median), or 10th (low) percentile. Variable survival represents a random draw from the posterior distribution describing the survival function. Shaded regions equal 90th percentiles from replicate runs.

been documented in other amphibian taxa (Phillips et al., 2002; Scott, 1990). This difference in size at metamorphosis is important because individuals emerging as larger metamorphs are sometimes able to reproduce as yearlings in their first year returning to the breeding pond, while smaller metamorphs do not breed until at least their second year (Haas, unpublished data). Even if larger individuals do not breed until their second year, the larger size at first reproduction should contribute to an overall increase in lifetime fitness (Berven, 1990; Semlitsch et al., 1988; Smith, 1987). Increasing the time available for larval development by improving hydrology through upland thinning (e.g., Jones et al., 2018) or the artificial extension of wetland hydroperiods offers a promising avenue for future conservation efforts (Mathwin et al., 2021). Other factors, including water temperature, the availability of prey, and the structure of the wetland habitat can also impact growth and size at metamorphosis in amphibians (Alvarez & Nicieza, 2002; Skelly et al., 2002). Flatwoods salamanders are now regularly being raised in mesocosms as part of ongoing conservation work, and experimental studies examining the effects of the larval environment on growth and survival are now possible.

Despite over 10 years of drift fence data, the current modeling framework was limited by key gaps in our basic natural history knowledge of flatwoods salamanders. First, there is considerable uncertainty in egg-laying behavior of female flatwoods salamanders, including the proportion of females breeding each season and whether eggs are always laid together or are sometimes dispersed (either spatially or temporally). These behaviors are likely to interact with breeding wetland hydrology to impact hatching success and survival to metamorphosis. Our models indicate that population growth is sensitive to the frequency of successful metamorphosis, and thus this is an important avenue for future field studies. Second, we did not account for either emigration or immigration of salamanders from one breeding site to another. While these processes are likely important at a landscape scale (Brooks et al., 2019), few observations of flatwoods salamanders moving between the two drift fenced wetlands have been recorded even though they are separated by just 250 m (Haas, unpublished data), making it challenging to meaningfully quantify these processes. Lastly, we did not explicitly incorporate the approximately 5-month period between metamorphosis and the following breeding season (i.e., models functioned on a year time step). The stochastic nature of recruitment in many ephemeral pond breeding amphibians is thought to be a rate-limiting step (Alford & Richards, 1999; Boone & Bridges, 2003; Kiesecker et al., 2001; Pechmann & Wilbur, 1994; Schmidt et al., 2002; Schmidt et al., 2005; Semlitsch, 2003; Wilbur, 1980; Wilbur & Collins, 1973). Post-metamorphic amphibians are generally considered to experience high predation and desiccation risk (Burrow et al., 2021; Messerman et al., 2020; Messerman & Leal, 2020, 2022; Roznik & Johnson, 2009), but data describing this portion of the life cycle are lacking in flatwoods salamanders. It is likely that some of this early post-metamorphic mortality was captured in our egg survival parameter as some estimates of survival to metamorphosis exceed 5%, however this deserves further investigation (Petranka, 1989; Shoop, 1974).

The quantity and quality of data required to construct useful demographic models is lacking for many amphibian species (Schmidt et al., 2005). Even for relatively well-studied species, datasets often lack the necessary coverage across multiple life stages or populations (Biek et al., 2002; Crawford et al., 2022; Messerman et al., 2023; Schmidt et al., 2002, 2005; Vonesh & De la Cruz, 2002). Our modeling results, for example, are based entirely on data from small wetlands because of the logistical constraints of conducting high intensity population monitoring in large wetlands. Additional long-term monitoring is needed to better understand the effects of wetland or population size and surrounding upland habitat conditions on flatwoods salamander viability. Given the challenge in parsing out natural fluctuations from population declines in many amphibian taxa (Alford & Richards, 1999; Chesson & Warner, 1981; Pechmann et al., 1991; Salvidio, 2009; Semlitsch et al., 1996; Vucetich & Waite, 1998; Whiteman & Wissinger, 2005), it remains surprising that long-term studies designed to obtain the demographic data required for projection models do not occupy a more prominent position in amphibian conservation. Our study highlights the usefulness of such long-term studies, the broad utility of demographic modeling, and the role that PVAs play in identifying, diagnosing, and combating global amphibian declines.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

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SUPPORTING INFORMATION

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