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RESEARCH

Historical surveys support population modeling in a woodland salamander: comparing age-structured and individual-based approaches

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Abstract

Population growth models are essential tools for predicting population demographic trends and assessing population viability over time. Population growth models are often parameterized using demographic data that account for imperfect detection; however, historical datasets—collected prior to the widespread incorporation of imperfect detection—may still yield valuable insights into long-term population dynamics. Here, we used a deterministic age structured model and a stochastic individual based model, which were both parameterized with age-specific vital rates, to estimate population growth in a woodland salamander (*Plethodon metcalfi*). To parameterize our model, we used long-term historical demographic data collected by Hairston (1983) to estimate population growth. Our objectives were to evaluate differences between the population growth models and assess whether historical demographic data can produce realistic estimates of population dynamics. We found that the individual based model predicted a declining population size, whereas the age structured model predicted an increasing population size. However, sensitivity analyses revealed that minimal changes to survival or fecundity were sufficient to produce stable populations in both models, reflecting observations of these populations in the wild. Therefore, our results suggest that historical data can be informative even in the absence of detection-corrected estimates in cryptic species. We also found that both models were capable of predicting age distributions similar to those observed in nature. Together, these results emphasize the importance of model selection and utility of historical datasets in forecasting population resilience under variable environmental conditions.

Keywords Individual based model · Age structured model · Vital rates · Lifetables · Stochastic · Deterministic

Introduction

Population growth models provide critical insight into the long-term stability of populations (Wisdom and Mills 1997). These models are used in a wide variety of contexts, such as evaluating the impact of environmental change, managing harvested populations, and predicting the effects of invasive species on native populations (Getz and Haight 1989; McRae et al. 2008; Ozgul et al. 2010). Population growth models also have varying levels of complexity, with some approaches, such as individual based models, including demographic parameters, environmental variability, genetic factors, and carrying capacity (Boyce 1992; Beissinger and McCullough 2002). Other approaches, such as age-structured population growth models, are more simplistic, incorporating fixed elements (i.e., stable environments and fixed traits) in population estimates. Despite their simplicity, age-structured models provide a clear and tractable framework for identifying key demographic drivers of population growth, making them especially useful for hypothesis testing, comparative studies, and informing early-stage management decisions. Due to rapid and ongoing environmental change, tracking the growth of these populations is important for conservation and species management plans, targeting populations at greater risk of collapse (Wisdom

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and Mills 1997; Gotelli and Ellison 2006; Buckley et al. 2010; Knoerr et al., 2022).

Population growth models are often used to estimate changes in population size through time, but methodological differences have important implications for the interpretation of model outputs. These models can be deterministic, where characteristics of the population are fixed, (such as age-structured/matrix models [ASM]; Wisdom and Mills 1997; Jackson et al. 2020; Knoerr et al., 2022; Wada et al. 2024) or stochastic, which includes variation in these traits (such as individual based models [IBM]; Rose et al. 1999; Breckling 2002; Black and McKane 2012). Both stochastic and deterministic models are parameterized using vital rates of populations (i.e., birth and death rates), but they differ in how they account for randomness or variability in these rates over time. For example, ASMs track population growth at the population level and assume that all individuals within the same age class are identical, resulting in the same output for each iteration of the model (Gotelli 1995). Alternatively, IBMs track population growth at the individual level, allowing for variation in birth, death, and other vital rates across individuals (Breckling 2002; Black and McKane 2012). As a result, IBMs may be more prone to population crashes due to stochastic fluctuations, especially when population sizes are small (Lande 1993). Comparisons between deterministic and stochastic models reveal that they can produce population growth estimates that are similar, often due to adjusting deterministic models to incorporate slight variation in demographic traits (i.e., environmental perturbations of population density and annual density dependence; Wilson, 1998; Sable and Rose 2008). Alternatively, these models can also produce different population estimates, likely driven by the stochastic nature of individual based models which may better reflect natural population dynamics (Zhou and Buongiorno 2004; Sable and Rose 2008; Fortin and Langevin, 2012). These differences suggest that model choice can influence final predictions of population growth.

Accurate estimates of population size for cryptic species require extensive detail of the current population structure and life history, such as age classes, survival, and birth and death rates, since as little as 10% of the population may be active during a given sampling event (Hocking et al., 2021). Woodland salamanders (genus *Plethodon*) are fossorial, nocturnal, and restrict activity to cool, moist environmental conditions (Spotila 1972; Feder 1983). When conditions are unsuitable (such as dry, warm, or windy nights), salamanders will remain in underground burrows (Taub 1961), which hinders detection and affects estimates of survival and abundance. Additionally, severe weather (such as winter storms) can result in population reductions, significantly influencing population estimates and detection capacity (Petranka 1979). Although statistical and survey-based methods have been developed to account for imperfect detection (Kéry et al. 2009; Delaney and Leung 2010; Martínez-Villegas et al. 2024), life tables for *Plethodon* were developed before these methods were available and may provide valuable insight into the species life history if thoroughly sampled (i.e., Hairston 1983). By incorporating these historical data, population growth models can be used to investigate population demographics and, if the population is stable, assess how closely the measured vital rates align with the true rates.

In this study, we used estimates of age-specific survival and fecundity measured by Hairston (1983) to estimate growth of a population of woodland salamander (*Plethodon jordani*) using both age-structured and individual based modeling approaches. At the time of surveys, the *P. jordani* species complex had yet to be broken into the current set of seven species. The populations in this study are now recognized as *P. metcalfi*, and activity surveys in the same region of western North Carolina suggest that the species is still very abundant (Moskwik 2014; Riddell and Sears 2015). Our goals were to (1) assess whether Hairston's (1983) measurements were capable of producing stable population size or positive population growth and (2) compare deterministic and stochastic models for estimating population growth. This study will provide valuable insight into the population trajectory of *P. metcalfi* and identify the effects of model selection on population growth estimates. In addition, these models will help evaluate whether Hairston's (1983) sampling methods, which were conducted without accounting for imperfect detection, can nonetheless yield realistic estimates of age-specific demographic parameters.

Methods

We used estimates of age-specific survival and fecundity collected by Hairston (1983) to develop our models (Table 1). In short, Hairston (1983) conducted nightly searches for *P. metcalfi* and collected individuals by hand annually from 1973 to 1981 in three counties in North Carolina: Cashiers, Hughes Ridge, and Courthouse Creek. He collected snout-vent length (SVL) and mass measurements for all individuals and used size at collection to estimate age. He anesthetized and formalin-fixed a subset of salamanders to study the reproductive cycle by measuring oocyte and testes development. He then used these data to estimate survival ($l(i)$) and fecundity ($b(i)$) of individuals throughout their lifespan and created a life table for the Courthouse Creek population of *P. metcalfi* (Tables 1 and 5 in Hairston 1983). We used these data to estimate population growth rates using an age-structured model (ASM) and an individual-based model (IBM).

Table 1 Survival (*l(i)*) and fecundity (*b(i)*) estimates provided by Hairston (1983) across ages (in years)

Ages (*i*)	Survival (*l*(*i*))	Fecundity (*b*(*i*))
0	1.000	-
1	0.837	-
2	0.305	-
3	0.147	-
4	0.119	0.784
5	0.096	0.841
6	0.078	1.767
7	0.066	1.84
8	0.053	1.909
9	0.043	1.988
10	0.035	2.079
11	0.028	2.117
12	0.023	2.154
13	0.019	2.188
14	0.015	2.23
15	0.012	2.265
16	0.01	2.293
17	0.008	2.325
18	0.006	2.354
19	0.005	2.384
20	0.004	2.411
21	0.003	2.437
22	0.003	2.458
23	0.002	2.483
24	0.002	2.505
25	0.001	2.519
26	0.001	2.545
27	0.001	2.565
28	0.001	2.595
29	0.001	2.607
30	0.001	2.618

Table 2 Distribution of age classes for the starting population of the individual based model and age-structure model

Ages	Proportion of starting population (*N*)
0–1	19% (170)
1–2	28% (250)
2–3	7% (63)
≥3*	46% (412)

*Adults were evenly divided across ages 3–30, with 15 individuals per age class for ages 3–22 and 14 individuals per age class for ages 23–30

To test the accuracy of our models in predicting population estimates, we recreated Fig. 3.3 from Gotelli (1995), which illustrates the growth of two hypothetical populations across four age classes using different starting population structures (data from Table 3.2 in Gotelli 1995). Both models successfully reproduced the trends shown in the original figure (Figure S1), providing confidence that our implementations are functioning as expected and consistent with established results.

Age-structured model

We predicted the population trajectory of *P. metcalfi* using a Leslie matrix, which models changes in population size across age classes based on age-specific survival and reproduction rates (Gotelli 1995). In a Leslie matrix, each column of the matrix represents the age at time t and each row represents the age at time $t+1$. Because *P. metcalfi* can survive up to 30 years (Hairston 1983), our matrix was a 29 by 29 age-structured matrix (age classes start at 1, not 0, and end at 30; Gotelli 1995). The subdiagonal of a Leslie matrix is the probability that an individual at age i survives to age $i+1$ (P_i) and is calculated as:

$$P_i = \frac{l\,(i)}{l\,(i-1)}$$

where *l(i)* is the probability of an individual surviving from birth to age *i*. The first row of the matrix represents fertility, or the contribution of newborns to the population. The fertility at age *i* is calculated as:

$$F_i = b\,(i)\,P_i$$

where *b(i)* is the number of offspring produced at age *i*. This equation accounts for the survival probability of an individual to age *i* when calculating the number of offspring produced at that age, since an individual must survive to reproduce.

We ran our ASM using custom code in Python (v. 3.12.5). We used a population size and age distribution similar to Hairston's (1983) report. We began with a population size of 895 individuals and calculated the average proportion of age classes across the sample years (see Supplemental file; Table S1). Table 2 shows the distribution of the starting population we used in the ASM. Because Hairston (1983) classified individuals into age classes of 0–1 year, 2–3 years, and adults (3–30 years), we have structured our data in the same way for consistency. We ran a single iteration of the model over 200 years, updating the population annually. We selected a 200-year timespan to allow the model to reach a stable age distribution and long-term growth trajectory, minimizing the influence of initial conditions. We also calculated the intrinsic rate of population growth (r) to assess whether the population was growing, declining, or remaining constant. We calculated r using the following equation:

$$r = \frac{1}{t} \times ln\left(\frac{N_t}{N_0}\right)$$

where t is the time, N_t is the population size at time t, and N_0 is the initial population size. We calculated r at each time

step, starting after the initial population boom ($t=25$), then averaged all values for an estimate of population growth rate.

Individual based model

In addition to the ASM, we developed an IBM to simulate population growth of *P. metcalfi* using Classes(). In Python, classes define blueprints for objects, allowing users to bundle data (attributes) and behaviors (methods) into reusable structures. This is especially useful for IBMs because each organism can be represented as an object with unique traits (e.g., age, reproduction, survival), making it easier to track and update individuals dynamically over time. The attributes of the individuals included age, age-specific survival rate, age-specific fecundity, and whether they were 'dead or 'alive'. We started with the same initial population in the IBM as we did in the ASM (Table 2) and tracked the population over 200 years.

The model begins by assigning each individual a probability of survival based on its age class (P_i). We implemented stochastic survival by drawing a random number from a uniform distribution between 0 and 1 for each individual. If the random number is less than or equal to P_i, the individual survives; otherwise, it dies (Hairston 1983). For example, if two individuals in the same age class each have a survival probability of 0.837, one might draw 0.3 and survive, while another draws 0.9 and does not. Although both individuals have the same survival probability, the model incorporates demographic stochasticity by allowing outcomes to vary across individuals and time steps, reflecting the role of chance in survival. Salamanders that did not survive were considered 'dead' and were removed from the population. Those that survived were then able to reproduce, with reproductive output also being dependent on age (*b(i)*). Any offspring created were added to the population with an age of 0. Because life tables report fractional egg production per year (e.g., 2.3 eggs), we assumed salamanders only produced integer-valued offspring counts. Any fractional offspring (e.g., 0.3) were carried over for each individual across years. Once the cumulative remainder exceeded 1, an additional offspring was added to that individual's reproductive output for the year, effectively modeling fractional reproduction as residual energy allocation. This approach aimed to better align the life history parameters of the ASM while accommodating the constraints of IBMs. Once reproduction occurred, the salamanders in the population increased their age (i) by one year ($i+1$), and we calculated the probability of survival from i to $i+1$ (P_i). Hairston (1983) did not provide variation in survival (*l(i)*) and fecundity (*b(i)*) values across life stages; thus, we decided not to arbitrarily implement individual variation in these parameters.

Each year over the 200-year simulation, the population underwent reproduction, aging, and the removal of deceased individuals. Due to variation in survival within each age class, the population size changed with each run of the model. Therefore, we ran 100 iterations of the model and averaged population size for each year over the 100 runs for an average estimate of the change in population size. We calculated r at each time step, starting after the initial population boom ($t=25$), for each iteration of the model then averaged across all values for a final estimate of growth.

Sensitivity analyses

We also evaluated the sensitivity of population growth to variation in vital rates by assessing whether the models could produce stable populations over time. This analysis was motivated by Hairston's (1983) report of long-term stability in the *P. metcalfi* population at Courthouse Creek (see Fig. 3 in Hairston 1983). By testing whether our models could replicate this observed stability, we aimed to assess their biological realism and responsiveness to parameter changes. Therefore, we ran sensitivity analyses that systematically increased or decreased Hairston's (1983) estimates of the probability of survival (P_i) and fecundity ($b(i)$) by 1% to assess the population's sensitivity to these changes in growth. For both models, we used the following equations to determine the adjusted P_i and *b(i)*:

$$P_{inew} = P_i + P_i \times \frac{x}{100}$$

$$b(i)_{new} = b(i) + b(i) \times \frac{x}{100}$$

where x increased from 0 to the value at which the population reached stable population growth. We reran the models for every incremental change in P_i and *b(i)* and reran the 100 iterations of the IBM for every incremental increase.

We also grouped salamanders into life stages and reran the above sensitivity analyses to determine whether population growth rates were more sensitive to changes in demographic rates in specific life stage groups. We grouped individuals based on reproductive outputs: individuals that did not reproduce were juveniles (0–3 years old), individuals that produced <2 offspring were young adults (4–9 years old), and salamanders that produced >2 offspring were adults (10–30 years old). We ran the survival sensitivity analysis for each group and ran the fecundity sensitivity analysis for the young adults and adults, since juveniles were not reproductively active. These life-state boundaries also correspond to major shifts in reproduction, including the onset of reproductive activity at 3 years and the approximate generation time of 10 years (Hairston 1983).

Distribution of population across age classes

We also compared the demographic structure of the modeled and observed populations of *P. metcalfi*. For the ASM, we calculated the proportion of individuals in each class for the final population (t=200). Based on the sensitivity analysis for the IBM, an increase in survival of 1% resulted in population growth similar to the ASM. Thus, we used the output from the original IBM and the output from the IBM with a 1% increase in survival to calculate the proportion of individuals in each class at the final population (t=200). We then compared the distribution of individuals across age classes between the ASM, IBM, IBM+1% survival, and Hairston's (1983) observed values. Because only a single estimate was available for each age class in the empirical data, we did not conduct a formal statistical analysis; instead, we qualitatively compared the distributions to assess the degree of similarity.

Results

Age-structured model

Results from the ASM indicated an increasing population (r=0.0028±0.0004 SD), with the population reaching over 2,000 individuals after 200 years (Fig. 1A). Because the model predicted population growth, we adjusted the sensitivity analysis to determine how much P_i and $b(i)$ would have to decrease to reach a stable population. This analysis indicated that fecundity ($b(i)$) and survival (P_i) estimates would need to decrease by less than 3% and 1%, respectively, for population growth to stabilize (Fig. 2A, B). When separating by age class, we found the juveniles and young adults needed a 1% decrease in the probability of survival for the population to decrease, and adults required a 2% decrease (Fig. 2C). For fecundity, young adults and adults required a 5% and 7% decrease, respectively (Fig. 2D).

Individual based model

Our IBM predicted a declining population (r = −0.0022±0.0026 SD), with an average final population size of 377 individuals (range: 50–853 salamanders) (Fig. 1B). At the beginning of the model, each iteration predicted a similar spike in population growth, followed by a steady decline. Population estimates began to diverge across the 100 iterations at the start of this decline, approximately 10 years after the start of the run (Fig. 1B). The sensitivity analysis indicated that fecundity and survival required less than a 4% and 1% increase, respectively, to reach a stable population (Fig. 2A, B). When we increased survival by 1%, the population growth trend was similar to the ASM (r=0.0070±0.003 SD; Fig. 1A, C), suggesting that both models are sensitive to small changes in vital rates and produce comparable growth trends. Average final population size for the IBM with a 1% increase in survival was 2,455 individuals (range: 1,245–3,985 salamanders) (Fig. 1C).

When separating the sensitivity analysis by life stage, we found that juveniles and young adults required a 1% increase in survival for the population to increase, and adults required a 2% increase in survival (Fig. 2C). Young adults and adults required a 8% and 6% increase in fecundity, respectively, for positive population growth (Fig. 2D).

Distribution of population across age classes

The IBM, the IBM with +1% survival, and the ASM produced similar age class distributions, but all models differed from the observed values at the youngest and oldest age classes. Specifically, the proportion of individuals in the 1–2 and 2–3-year age classes was similar across all four sources

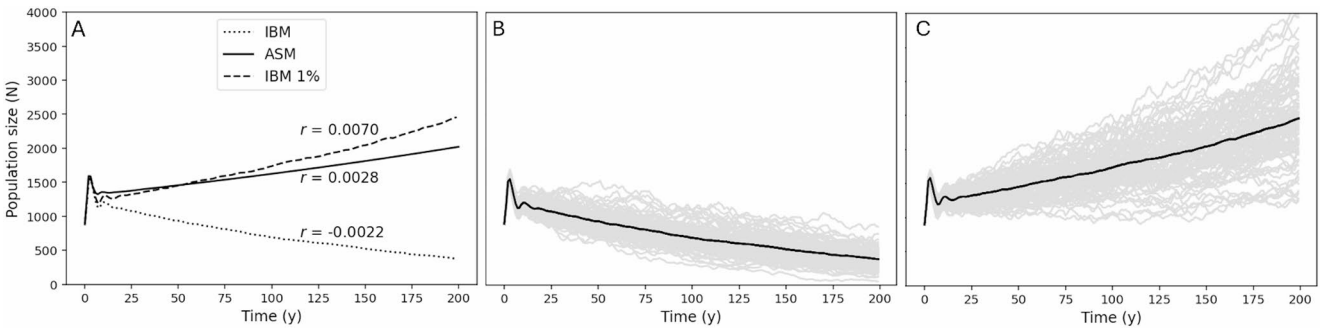

Fig. 1 Estimated population trends of *Plethodon metcalfi*. (**A**) Population trends from the age-structured model (ASM; solid line), individual based model (IBM; dotted line), and the IBM with a 1% increase in the probability of survival (IBM 1%; dashed line) using Hairston's (1983) original estimates for survival (P_i) and fecundity ($b(i)$). r indicates the intrinsic rate of growth of the population. Negative r symbolizes population decline in the IBM, and positive r indicates population growth in the ASM and IBM 1%. (**B**) Population decline for each of the 100 iterations of the IBM model (gray lines) and the average estimate of population decline (black line). (**C**) Population growth for each of the 100 iterations of the IBM model with a 1% increase in survival (gray lines) and the average estimate of population growth (black line)

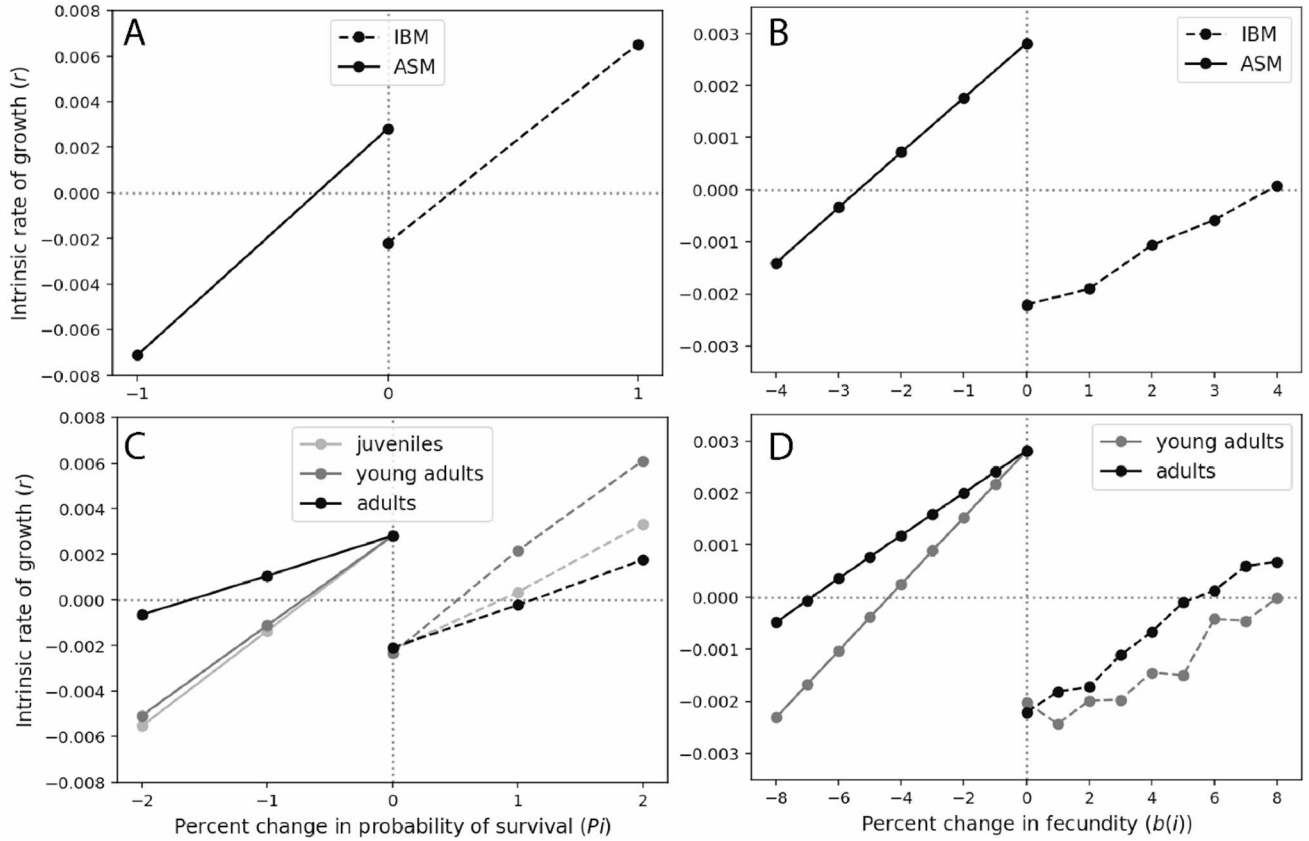

Fig. 2 Population growth of *Plethodon metcalfi* measured with different survival (P_i) and fecundity ($b(i)$) values across the whole population (**A**, **B**) and across specific life stages (**C**, **D**). The x-axis shows the percentage that (**A**, **C**) P_i and (**B**, **D**) $b(i)$ must change for stable, positive, or negative population growth (measured as the intrinsic rate of growth (r)). The vertical dotted line represents r using the original vital rates (no change in survival and fecundity), and the horizontal dotted line represents an r of zero, at which point the population would be stable. Values below this line represent population decline ($r<0$), and values above this line represent population growth ($r>0$). Dotted lines in **C**, **D** represent results from the IBM, and solid lines represent results from the ASM. There are no juveniles in **D** because they are not reproductively active and thus are not affected by changes in fecundity

(1–2: 28–30%; 2–3: 7–11%; Fig. 3). However, the models predicted a higher proportion of 0–1-year-olds (30–34%) and a lower proportion of adults (27–29%) compared to the empirical data (0–1-year-olds: 19%; adults: 45%; Fig. 3).

Discussion

Life tables collected prior to the use of imperfect-detection methods can still offer valuable insight into population demographics. In this study, we estimated growth of a woodland salamander population using historical data in two modeling approaches: an individual-based model and deterministic age-structured model. Despite the models producing opposite population trends (Fig. 1), our sensitivity analyses revealed that the changes in survival (P_i) and fecundity ($b(i)$ needed to reach a stable population were minimal and similar across both models (<1% for survival and <3–4% for fecundity; Fig. 2AB). We found similar trends when separating individuals into life stages (Fig. 2C, D). Because Hairston's (1983) surveys indicated that the population was stable, these results suggest that both models are capable of producing ecologically realistic outcomes with only minimal adjustments to the vital rate estimates. These results also highlight the value of historical data since both models were able to produce similar estimates of population growth compared to those observed by Hairston (1983). Hairston's (1983) surveys occurred over eight years, which is sufficient for detecting population trends in *Plethodon* (Luymes and Chow-Fraser, 2019). Thus, the original survey data likely captured meaningful signals of long-term population dynamics and serve as a valuable point of comparison for our simulated results. The demographic parameters collected by Hairston (1983) were likely accurate due to the high sampling effort over time, though more modern statistical approaches likely require less data to produce similar demographic estimates (Bailey et al. 2004; Connette et al. 2015; Caruso et al. 2020). Thus, life history tables are a

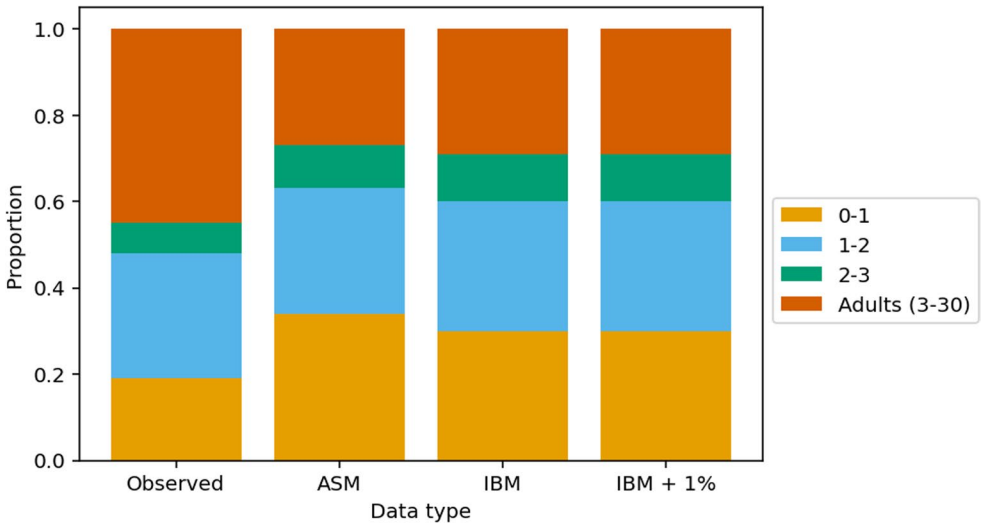

Fig. 3 Distribution of age classes (years) in the observed population (Hairston 1983), the age-structured model (ASM), the individual based model (IBM), and the IBM with a 1% increase in the probability of survival

valuable resource for estimating population dynamics, even in the absence of correcting for detection.

Discrepancies between modeled and observed age class proportions are likely driven by challenges in accurately detecting salamanders in the field. Juvenile salamanders (0–1-year-olds) are much more difficult to detect compared to older individuals. They are smaller, have lower activity, and prefer deeper microhabitats (e.g., under leaf litter or below the soil surface) compared to older individuals (Semlitsch 1980; Kramer 1996; Ash 2019), resulting in low detection probability. Hairston (1983) also relied on morphological traits to assign age classes (Semlitsch 1980; Marvin 1996; Buderman and Liebgold 2012; Riedel et al. 2012), which may have resulted in misclassification of individuals due to size differences (Marvin 2001; Leclair et al. 2006). Lastly, the number of juveniles Hairston (1983) detected was lower on certain years, suggesting he may have sampled in years following poor recruitment whereas our models likely simulate average dynamics. The mismatch between observed and modeled distributions illustrates how simulation-based approaches can complement field data by offering testable hypotheses about population structure, demographic bottlenecks, or detection probability. Comparing observed population demographics with modeled outputs may provide additional insight into population structure that may be missed through observation alone.

Whether one uses a deterministic or stochastic demographic model should depend on the purpose of the model as well as the study system under investigation. Deterministic matrix models operate on expected values rather than simulating individual outcomes, resulting in faster, more efficient models (Breckling 2002). Additionally, certain matrix models (i.e., stochastic models) incorporate environmental and demographic variability, allowing for stochasticity when estimating population growth (Buckley et al. 2010; Jackson et al., 2020). All matrix models treat individuals within the same age class as homogeneous units, excluding the effects of individual variation. In large populations, this simplification may have minimal impact on overall population estimates (Ramula et al. 2009; Buckley et al. 2010); however, in smaller or more vulnerable populations, individual variation can significantly influence demographic outcomes (Gabriel and Bürger 1992). Individual based models have the potential to address this concern by simulating population growth using individuals (Breckling 2002; Black and McKane 2012) and assigning a suite of characteristics unique to that individual. However, the application of IBMs is often constrained by the need for variation in individual traits or age-specific vital rates to parameterize the models, as well as requiring greater computation power due to the nature of tracking each individual through its lifespan (Breckling 2002). Thus, model selection also depends on the resources available for the population of interest. For example, matrix models would be best applied if computational power is limited, when producing demographic estimates of larger populations, and if there is limited (or no) variation in population traits and vital rates. IBMs may be preferable in contexts with few computational constraints, relatively small population sizes, or substantial variation in predicted vital rates or individual-level traits. Determining which model is best depends on the specific question and study system being investigated because of the underlying differences between model structures and requirements.

Life-table elasticity describes how proportional changes in vital rates, such as survival or fecundity, affect the proportional change in population growth rate (Caswell 2001; de Kroon et al. 1986). Although small adjustments to either parameter may seem negligible, sensitivity analyses show that population growth rates in long-lived species can be highly responsive to small changes in both survival and

fecundity, with survival having a greater sensitivity than fecundity (Heppell et al. 2000; Sæther and Bakke 2000). This arises because survival probabilities and fecundities jointly determine the cumulative reproductive output across an individual's lifetime, and changes in either parameter propagate through multiple age classes and can substantially alter the net reproductive rate. Here, we found that fecundity and survival required less than 3–4% and less than 1% change, respectively, to alter the population trajectory in both the ASM and IBM. We found similar results when separating salamanders into life stages, with survival requiring less than 1–2% change and fecundity less than 5–8% change. Thus, both models support that salamander populations may be highly sensitive to small changes in vital rates, suggesting that the focal population may be near demographic equilibrium since minimal changes were needed to alter the population trajectory.

Sensitivity analyses can also indicate which portions of the population drive more variation in population growth rate, thus influencing changes in population trajectory (Reed et al. 2009; Wolf et al. 2014; Mortensen and Reed 2016). Here, we found that population growth was more sensitive to changes in survival for juveniles and young adults compared to adults, likely because these younger age classes constitute a greater proportion of the population. This trend is also present in population growth models for other amphibian species (Vonesh and De La Cruz, 2002; Trenham and Shaffer 2005), although in other cases, population growth rates are equally sensitive to changes in demographic rates across age classes (Biek et al. 2002; Kissel et al. 2014). For fecundity, our models diverged slightly, with the ASM indicating population growth was more sensitive to fecundity in young adults, whereas the IBM indicated that adults had a greater impact. This separation may be driven by the fractional offspring production in the IBM or by other differences between model types (i.e., tracking population growth by individuals [IBM] or by age classes [ASM]). Understanding the sensitivity of populations to changes in vital rates can allow for targeted management efforts of specific populations or life stages within populations that drive growth. Population growth models are used in a variety of contexts, including tracking growth in fisheries, forestry, and forecasting the risk of population extinction due to climate change (Wisdom and Mills 1997; Pethybridge et al., 2013; Jackson et al., 2020; Wada et al. 2024). Here, we relied on life table estimates collected by Hairston (1983) to track population growth of a woodland salamander (*Plethodon metcalfi*) using both age structured and individual based models to determine the ability of historical datasets to predict known population patterns. Although we found that the two models predicted opposite trends of population growth, Hairston's (1983) estimates required minimal adjustments to reach a stable population, highlighting the accuracy of these historical estimates. This suggests that populations may be sensitive to small changes to survival and fecundity, implying that natural and anthropogenic disturbances can have important impacts on the stability of woodland salamanders. In fact, abundance estimates of *Plethodon cinereus* reduced by 76% following anthropogenic disturbances (forest harvesting), with approximately 60 years needed for the population to recover to pre-disturbance abundances (Homyack and Haas, 2009).Thus, species' susceptibility to population declines will likely increase with the higher frequency of extreme climate events and anthropogenic disturbances (Venter et al. 2016; Ummenhofer and Meehl 2017). Modern statistical techniques and population modeling approaches offer the opportunity to leverage long-term, historical demographic data (i.e., Hairston 1983) to estimate population growth and assess species' resilience to environmental change. Although these historical data were collected prior to the widespread incorporation of imperfect detection in demographic surveys, our findings suggest that they yield meaningful estimates of population growth when combined with appropriate modeling frameworks and assumptions. These findings also imply that historical demographic parameters can be used to evaluate differences in population growth among sites or to track temporal changes within the same population. Furthermore, such data can be used to quantify the sensitivity of population dynamics to variation in key vital rates. As environmental and landscape conditions continue to shift, forecasting population stability becomes critical for informing conservation strategies and prioritizing management efforts for populations most vulnerable to decline.

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Data availability The python script to run the above models is available at https://osf.io/qn4se/overview? view_only=6bba843ba72841d4b3ac0a90d3160a31.

Declarations

Competing interests The authors declare no competing interests.

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Supplemental Information

Calculating distribution of individuals across age classes

Hairston (1983) provided estimates of the proportion of individuals across age classes and the number of individuals in each age class (Table 6: 0-1-year-olds; Table 7: 1-2- and 2-3-year-olds and adults). We used the data from these tables to estimate the number of individuals in our starting population and the proportion of individuals across the population (data provided in Table S1).

Proportion of individuals in each age class

We used data from the Courthouse Creek population in Table 6 to calculate the proportion of 0-1-year-olds to include in the models. We averaged over the monthly proportions of the 5-year estimates of 0-1 year olds (Table S1):

$$0-1\ year\ olds\text{:}\ \frac{0.045+0.233+0.425}{3}=0.23$$

For the remaining salamanders, we used data from the Courthouse Creek population in Table 7 and averaged across monthly proportions (Table S1):

$$1-2\ year\ olds\text{:}\ \frac{0.360+0.421+0.271}{3}=0.35$$

$$2-3\ year\ olds\text{:}\ \frac{0.135+0.058+0.047}{3}=0.08$$

$$adults\text{:}\ \frac{0.505+0.521+0.682}{3}=0.57$$

Once we had the proportions for each age class, we summed the values to determine if they equaled one.

$$0.23+0.35+0.08+0.57=1.23$$

In order to obtain true proportional data (ranging from 0-1), we then divided the calculated proportions by 1.23 for a final estimate of the proportion of individuals in each age class (see Table 2 for final proportions).

Number of individuals in the population

Similar to above, we used data from the Courthouse Creek population in Tables 6 and 7 (Hairston, 1983) to estimate the total number of individuals for our starting population. We used the 5-year estimates of 0-1-year-olds and divided each value by 5, producing a yearly estimate of the number of 0-1-year-old individuals for each season (Table S1; May-June: 202 salamanders; July – Aug: 206 salamanders; Sept – Oct: 133 salamanders). We then added these values to the total number of individuals in the remaining age classes (Table S1; May – June: 1,170

salamanders; July – Aug: 997 salamanders; Sept – Oct: 517 salamanders.) Lastly, we averaged over these values for a final estimate of population size to include in our model (N = 895).

Table S1: Data from Tables 6 & 7 in Hairston (1983) used to calculate the starting population size and the proportion of individuals in each age class for the ASM and IBM models. Data for 1-year-olds are over 5 years. Data for the remaining age classes are based on a one-year assessment of population size.

Age class	May-June		June-Aug		Sept-Oct	
	N	Proportion	N	Proportion	N	Proportion
5-year estimates for 0-1-year-olds	1014	0.045	1031	0.233	668	0.425
1-2-year-olds		0.360		0.421		0.271
2-3-year-olds	968	0.135	791	0.058	384	0.047
adults		0.505		0.521		0.682

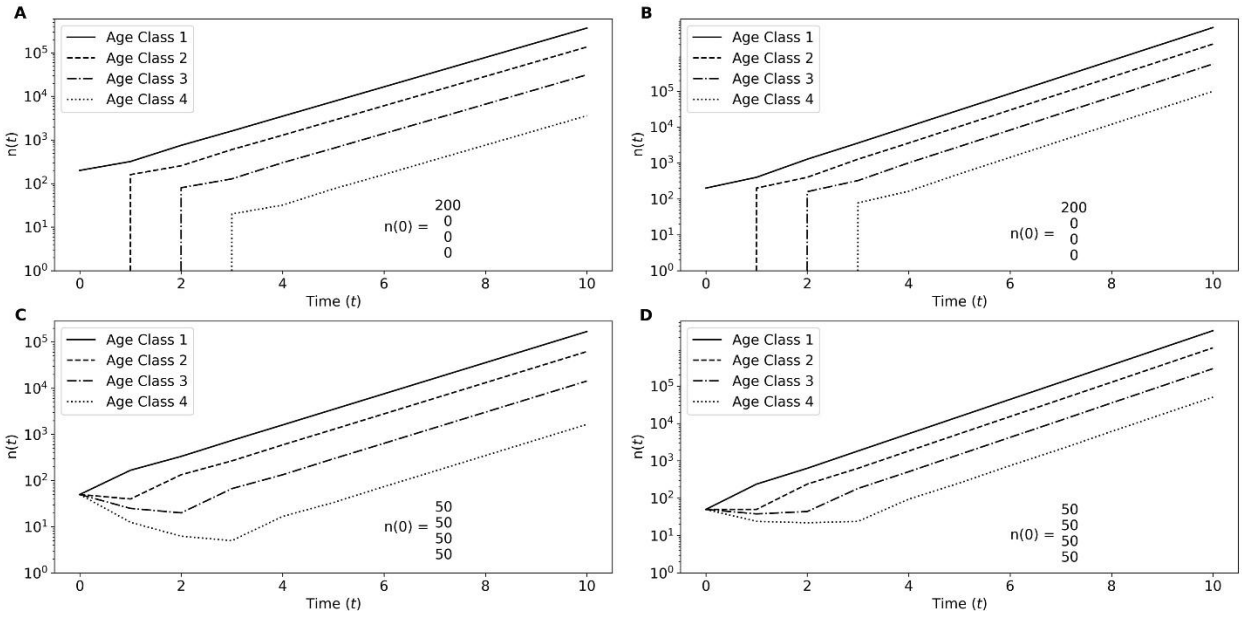

Fig S1 Recreating Figure 3.3 in Gotelli (1995) using age-structured models (ASM) and individual-based models (IBM). Population growth estimates of hypothetical populations using ASMs (A & C) and IBMs (B &D). Age classes are shown by the different line types, and the starting populations are in the bottom right corner. Figures A & B started with 200 individuals in the first age class and no individuals in the remaining age classes, and figures C & D started with 50 individuals in each age class. The ASM figures (A & C) replicate the figures found in Gotelli (1995). Population estimates produced using the IBM were higher by the final timepoint compared to populations estimates produced using the ASM. Across all figures, population growth stabilized into identical age distributions after initial fluctuations. Note that the y axes are on the logarithmic scale and therefore indicate exponential growth of the populations