

Variation in Flatwoods Salamander Survival Is Unrelated to Temperature and Rainfall

Authors: Brooks, George C., Gorman, Thomas A., and Haas, Carola A.

Source: Ichthyology & Herpetology, 112(1) : 31-40

Published By: The American Society of Ichthyologists and Herpetologists

URL: <https://doi.org/10.1643/h2020131>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Variation in Flatwoods Salamander Survival Is Unrelated to Temperature and Rainfall

George C. Brooks¹, Thomas A. Gorman², and Carola A. Haas¹

Survival rates are known to vary over the course of an individual's lifetime and among individuals within a population. Quantifying the natural variability in survival rates is crucial when scaling up to infer the dynamics of populations. Using ten years of mark–recapture data from two adjacent wetlands on the Florida Panhandle, we investigated individual and temporal variability in survival rates of Reticulated Flatwoods Salamanders (*Ambystoma bishopi*). Our objectives were to 1) provide the first estimates of survival for the species, 2) evaluate the relationship between body size and mortality risk, 3) quantify the degree of variability in survival rates across the study period, and 4) discern whether variability in survival or detection correlates with environmental conditions. To address these objectives, we constructed a modified Cormack–Jolly–Seber model that includes body size and year as covariates. Mean annual survival was estimated to be 0.72 and was strongly correlated with body size; survival rates of the smallest individuals in the study were 0.5 and those of the largest individuals were 0.85. Survival also varied considerably across years, but it did not correlate with temperature extremes or rainfall. Therefore, a key priority for future research should be to identify the ecological correlates of mortality risk in *A. bishopi*. Our results can be integrated into demographic projections for Reticulated Flatwoods Salamanders and will help managers to discern population viability, evaluate alternative management strategies (e.g., habitat restoration), or buffer the impacts of climate change. More broadly, our work highlights the need for more long-term studies that will garner accurate estimates of vital rates to aid ongoing recovery efforts for endangered and at-risk species.

SURVIVAL rates are known to vary over the course of an individual's lifetime and among individuals within a population (Roff, 1992; Cooch, 2002; Ebenman and Persson, 2012). Mortality risk is intrinsically tied to environmental conditions and body size and can therefore show considerable variability through time and across a population (Laurie and Brown, 1990; Forsman, 1991; Sorci and Clobert, 1999; Kunz and Ekman, 2000; Church et al., 2022). For instance, in amphibians, regulating temperature and water balance is more challenging for smaller individuals, making them susceptible to prolonged periods of drought, temperature extremes, and food deprivation (Ash et al., 2003; Knapp et al., 2003; Rothermel and Semlitsch, 2006; Tilghman et al., 2012). In addition, body size can directly influence an individual's vulnerability to gape-limited predators, such that smaller individuals experience higher mortality than larger individuals (Shine, 1991; Janzen, 1993; Forsman, 1996; Sorci and Clobert, 1999; Lind et al., 2008; Kishida et al., 2009).

Quantifying the natural variability in survival rates is crucial when scaling up to infer the dynamics of populations (Brooks et al., 2000; Rees and Ellner, 2009). Certain life histories can be extremely sensitive to changes in vital rates, and stochastic forces strongly impact population growth (Lande, 1993; Letcher and Horton, 2008; Van de Wolfshaar et al., 2008; Rees and Ellner, 2009; Xu et al., 2010). By treating survival as a fixed parameter, traditional demographic methods used to conduct population viability analyses may generate erroneous conclusions regarding population status and extinction risk (Ramula et al., 2009; Hegg et al., 2013). In the context of modern conservation efforts, assessments that neglect variation in mortality could lead to flawed management decisions, thereby reducing the effectiveness of conservation measures for at-risk species.

For studies with infrequent sampling events or low capture probabilities, however, discerning the relationship between survival and ecological covariates is often difficult to achieve (Wulfsohn and Tsiatis, 1997; Su and Wang, 2012; Langrock and King, 2013; Rose et al., 2018). Capture–recapture data sets are largely comprised of partial records, including individuals that were born prior to the start of the study, individuals that die after the study has ended, and instances that simply went unobserved (Lebreton et al., 1992; Pike et al., 2008; Royle, 2008; Papadatou et al., 2012; Rose et al., 2018). Historically, records such as these were often omitted from analyses (Bailey et al., 2004; Matechou et al., 2013), or it was necessary to assume survival rates were constant for models to be identifiable (Pollock et al., 1990). Methodological advances have allowed for the inclusion of more partial records in mark–recapture models (Pledger et al., 2003, 2010; Colchero and Clark, 2012; Su and Wang, 2012), but challenges remain (Letcher and Horton, 2008; Gilroy et al., 2012; Barbour et al., 2013; Ergon and Gardner, 2014). Notably, if ecological covariates impact both mortality risk and animal behavior, models may inadvertently conflate variation in survival with variation in detectability (Kellner and Swihart, 2014).

Amphibians exemplify the challenges associated with obtaining survival estimates from wild populations. Many amphibians are long lived, sometimes surviving for multiple decades in their terrestrial life stage (Duellman and Trueb, 1994; Petranka, 1998; Wells, 2019). Thus, there is a potential for significant variability in survival rates, which in turn has strong implications for population growth (Biek et al., 2002; Vonesh and De la Cruz, 2002; Harper et al., 2008; Terrell et al., 2023). Both survival and activity periods of amphibians are impacted by climatic factors (e.g., Brooks et al., 2019; Cayuela

¹ Virginia Tech, Department of Fish and Wildlife Conservation, 310 West Campus Drive, Blacksburg, Virginia 24060; Email: (GCB) boa10gb@vt.edu; and (CAH) cahaas@vt.edu. Send correspondence to GCB.

² Washington State Department of Natural Resources, Aquatic Resources Division, Olympia, Washington 98504; Email: thomas.gorman@dnr.wa.gov. Submitted: 16 September 2020. Accepted: 15 November 2023. Associate Editor: J. Kerby.

© 2024 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/h2020131 Published online: 13 February 2024

et al., 2020; Messerman et al., 2020; Sanchez et al., 2020), and a positive relationship between body size and vulnerability to abiotic conditions has been shown for a variety of species (Spotila, 1972; Maiorana, 1976; Duellman and Trueb, 1994; Cabrera-Guzmán et al., 2013; Yagi and Green, 2017; Messerman et al., 2020). However, the fossorial nature of many amphibians makes it hard to disentangle environmentally driven variation in survival from the environmental correlates of aboveground activity and detection (Pollock, 1982; Petranksa, 1998; O'Donnell and Semlitsch, 2015; Burrow et al., 2021).

Using ten years of mark–recapture data from Eglin Air Force Base on the Florida Panhandle, we investigated individual and temporal variability in survival rates of Reticulated Flatwoods Salamanders (*Ambystoma bishopi*), a species endemic to the Southeastern United States. Reticulated Flatwoods Salamanders breed in ephemeral wetlands, a strategy that exhibits sporadic recruitment (Palis et al., 2006; Taylor et al., 2006; Brooks et al., 2020). Reticulated Flatwoods Salamanders are a federally listed endangered species, but recovery of the species is hampered by a lack of basic natural history information, including accurate survival estimates (USFWS, 2009, 2020). We constructed a modified Cormack–Jolly–Seber model that included body size and year as covariates. Our objectives were to 1) provide the first estimates of survival for Reticulated Flatwoods Salamanders, 2) evaluate the relationship between body size and survival, 3) quantify the degree of variability in survival and detection across the study period, and 4) discern whether variability in survival or detection correlates with environmental conditions. We predicted relatively high survival estimates, a positive association between survival and body size, and variability in survival and detection probabilities corresponding to extremes of temperature and precipitation. Our findings can be used to evaluate the long-term viability of Reticulated Flatwoods Salamander populations and help to inform ongoing recovery efforts.

MATERIALS AND METHODS

Study site.—Data were collected from a ten-year mark–recapture study of Reticulated Flatwoods Salamander populations on Eglin Air Force Base, Florida. Eglin is a large military installation (188,459 ha) primarily consisting of actively managed Longleaf Pine (*Pinus palustris*) dominated sandhills (approximately 145,000 ha) interspersed with treeless open test ranges, pine plantations, and mesic flatwoods. The landscape is punctuated by ephemeral wetlands which fill with late fall or early winter rains and typically remain inundated throughout the spring (Chandler et al., 2016, 2017). Wetlands in this region are typically characterized by open overstories dominated by Longleaf Pine, Slash Pine (*Pinus elliotii*), and Pond Cypress (*Taxodium ascendens*), with abundant herbaceous groundcover (including species of *Aristida*, *Dicanthelium*, and *Eriocaulon*). Long-term average temperatures for the region are 28°C in summer and 16°C in winter. Average precipitation is 166 cm annually.

Two Reticulated Flatwoods Salamander breeding wetlands have been completely encircled with drift fences and monitored since 2010 (see Erwin et al., 2016 and Brooks et al., 2019 for details). 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 spring) due to suitable hydrologic conditions. Upon capture of an individual salamander, we recorded the date and time of capture, and uniquely marked each individual using passive integrated transponder (PIT) tags (Biomark MiniHPT8 FDX-B) or visual implant elastomer (VIE; Northwest Marine Technologies, Inc.). We measured snout–vent length (SVL), total length, and mass of all animals captured at drift fences. By sampling repeatedly across years, we were able to generate a unique capture history for each marked individual. All field work was approved by the Virginia Tech Institutional Animal Care and Use Committee.

Statistical analysis.—We fit a hierarchical Cormack–Jolly–Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) to estimate annual survival and detection probabilities. We chose this approach because the CJS formulation can easily be modified to include continuous covariates and random effects while accounting for imperfect detection. We adopted a two-stage approach that first involves imputing values for unobserved body sizes, followed by a partial likelihood approach to estimate parameters of interest (Tsiatis et al., 1995; Su and Wang, 2012; Rose et al., 2018). Our formulation consists of a model for the partially observed state of each individual (the “process model”) and an observation model that accounts for imperfect detection, conditional on true state. Individual states, $z_{i,t}$, describe whether individual i is alive and available for capture at time t . An individual's state $z_{i,t}$ is modeled as

$$z_{i,t} | z_{i,t-1}, \phi = \begin{cases} 1 & , t = 1 \\ \text{Bern}(z_{i,t-1} \times \phi_{i,t}) & , t > 1 \end{cases}$$

where ϕ represents survival probability and $z_{i,t-1}$ is the state of individual i in the previous time step. We modeled survival as a linear function of body size at time of capture using a logit link function:

$$\text{logit}(\phi_{i,t}) = \mu_t + \beta X + \varepsilon_t$$

$$\mu_t = \log\left(\frac{\bar{\phi}}{1 - \bar{\phi}}\right)$$

$$\bar{\phi} \sim U(0, 1)$$

$$\beta \sim N(0, 1)I(0, \infty)$$

$$\varepsilon_t \sim N(0, \sigma^2)$$

$$\sigma^2 \sim \text{gamma}(1, 1)$$

where β is the slope for size-specific survival, μ_t is the intercept at time t , and X is a matrix of body sizes for every individual at each sampling period. Size measurements were standardized by subtracting the mean size of all captured individuals and dividing by the standard deviation, resulting in a transformed covariate with mean zero. Size estimates for unobserved individuals were interpolated using parameters estimated from the von Bertalanffy growth equation (von Bertalanffy, 1938; Brooks et al., 2020). Error (ε) was assumed to be normally distributed with mean zero and standard deviation σ^2 .

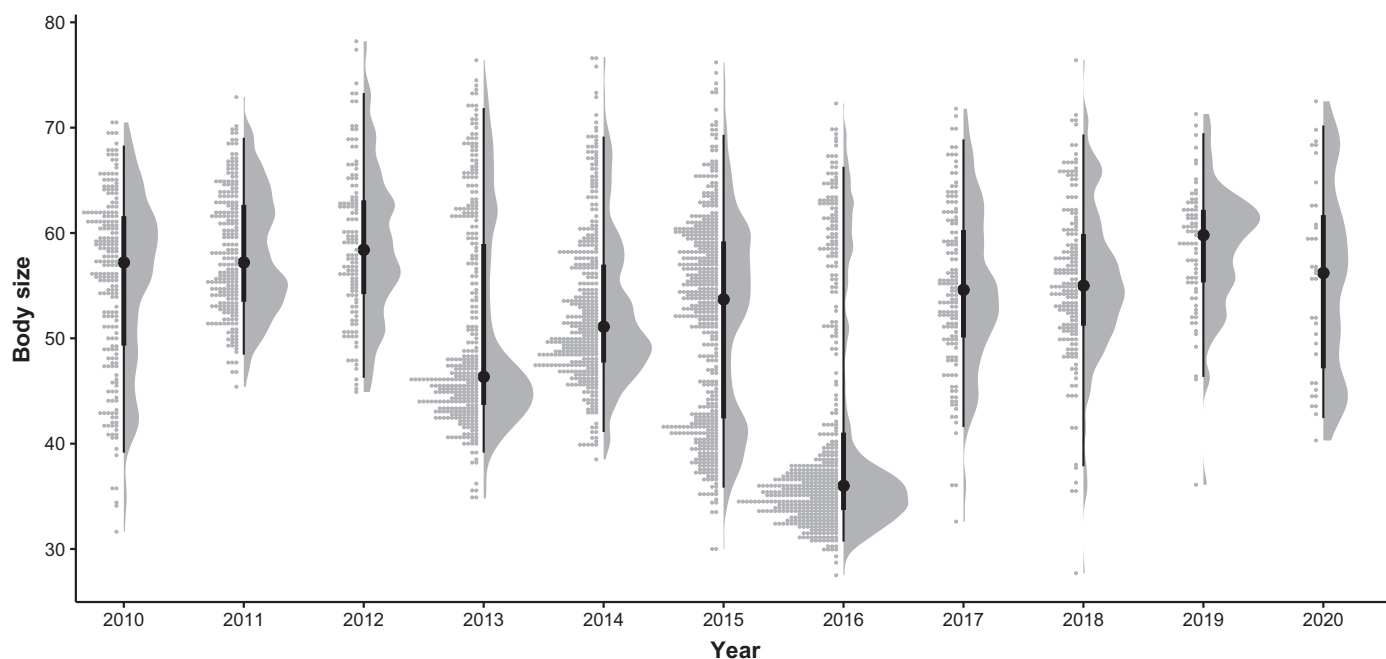


Fig. 1. Body size distributions for Reticulated Flatwoods Salamanders by year. Sizes are snout–vent length (SVL) in millimeters. Points represent the raw data points; the center lines show mean, 75%, and 95% confidence intervals; and the shaded region is an approximate density.

For each sampling occasion, an individual is either seen or not seen. Before an individual has entered the population, or after an individual has died, detection probability is zero. We used a non-informative prior on detection probability and compared scenarios with constant detection and scenarios where detection varied across years. Observed states for each individual ($y_{i,t}$) are linked to true states in the process model with a Bernoulli function:

$$y_{i,t} | z_{i,t} \sim \text{Bern}(z_{i,t} \times p_t)$$

$$\text{logit}(p_t) = \omega + \epsilon_t$$

$$\omega = \log\left(\frac{\bar{p}}{1 - \bar{p}}\right)$$

$$\bar{p} \sim U(0, 1)$$

$$\epsilon_t \sim N(0, \sigma^2)$$

$$\sigma^2 \sim \text{gamma}(1, 1)$$

where p is the probability of detection given an individual is available for capture and ϵ_t is the random effect of year on detection probability.

To assess the environmental basis of variation in survival and detection, we estimated the correlation between parameter estimates and temperature and precipitation data obtained from the PRISM Climate Group (Oregon State University, <https://prism.oregonstate.edu>). We downloaded monthly precipitation and temperature data from PRISM at the highest resolution (800 m) for our study area covering the years 2010 to 2020. We then calculated mean temperatures and total precipitation for June through August of each year to characterize the severity of summers across the study and calculated the mean temperature and total

precipitation for November through February of each year to characterize the severity of winters. We then determined to what degree annual survival and detection estimates were correlated with mean summer temperature, total summer precipitation, mean winter temperature, and total winter precipitation using Kendall's τ statistic. All analyses were performed in R using the package *R2WinBUGS* (Sturtz et al., 2005; R Core Team, 2022). Results reported are posterior means and 95% credible intervals unless otherwise stated.

RESULTS

Between fall 2010 and spring 2020, 953 adult salamanders at two breeding wetlands on Eglin Air Force Base were marked and released. Of the 953 animals marked, 688 marked individuals were recaptured on at least one subsequent occasion. The longest recorded time between two capture events was ten years. In addition, 704 metamorphs were captured emerging from wetlands but were excluded from subsequent analyses to avoid bias introduced by unequal emigration rates. Over the entire study duration, only 59 individuals tagged as metamorphs were ever recaptured. The average snout–vent length (SVL) of marked individuals was 54 mm (range = 32–76 mm; Fig. 1). The sex of 77% of individuals could be identified. Of the animals that could not be sexed, 24% were identified as yearlings (based on color pattern). Females on average were larger than males ($t = 13.4$, $df = 247$, $P < 0.001$) and individuals of unknown sex ($t = 13.4$, $df = 320$, $P < 0.001$), and the average size of males was larger than individuals of unknown sex ($t = 4.1$, $df = 272$, $P < 0.001$; Table 1, Fig. 2). Sex ratios approximated 1:1 at the start of the study but fluctuated across years. In 2014–2015, there were almost three males for every female, but in subsequent years the population was female biased (Table 1).

All parameters of the Cormack–Jolly–Seber model adequately converged; all potential scale reduction factors (PSRF) for individual parameters were < 1.1 . The multivariate PSRF for the

Table 1. Summary of Reticulated Flatwoods Salamander encounters at drift fences each year. Numbers are the number of unique individuals captured. Numbers in parentheses are the number of recaptures, i.e., animals that had been marked in previous years. Reported sizes are mean snout-vent length (SVL) in millimeters with associated standard deviations.

| Season | Number of females | Mean female size | Number of males | Mean male size | Sex ratio M:F |
|--------|-------------------|------------------|-----------------|----------------|---------------|
| 2010 | 67 (0) | 61.1±4.6 | 77 (0) | 54.0±7.6 | 1.1:1 |
| 2011 | 69 (20) | 60.4±6.2 | 71 (18) | 56.3±4.6 | 1:1 |
| 2012 | 43 (21) | 61.1±7.6 | 41 (24) | 57.0±6.3 | 1:1 |
| 2013 | 34 (26) | 65.3±5.4 | 22 (19) | 58.7±5.5 | 0.6:1 |
| 2014 | 46 (25) | 60.6±7.7 | 131 (11) | 50.6±5.0 | 2.8:1 |
| 2015 | 89 (19) | 59.4±5.6 | 64 (37) | 54.8±5.0 | 0.7:1 |
| 2016 | 40 (29) | 62.8±4.0 | 29 (19) | 57.1±5.7 | 0.7:1 |
| 2017 | 40 (9) | 60.9±5.9 | 48 (6) | 51.7±4.6 | 1.2:1 |
| 2018 | 53 (21) | 58.9±6.1 | 33 (14) | 52.4±3.6 | 0.6:1 |
| 2019 | 28 (18) | 60.7±4.8 | 12 (8) | 55.7±5.0 | 0.4:1 |
| 2020 | 9 (8) | 63.4±5.8 | 6 (2) | 51.1±4.9 | 0.7:1 |

full model was 1.06. Posterior P -values for survival and detection probabilities all approximated 0.5, indicating a good model fit. Owing to the model formulation, the parameters for survival and detection probabilities in the final year of the study were unidentifiable, and thus not reported here, nor used to calculate averages across years.

Estimated annual detection probabilities were 0.75 (CI: 0.66–0.82; Supplemental Fig. 1; see Data Accessibility). Thus, three years of monitoring on average would be required to achieve >95% detection probability for a given individual. However, two individuals went ten years between successive captures. The probability of detection varied across years. Detection was lowest in 2019 (mean = 0.61, CI: 0.45–0.76) and highest in 2015 (mean = 0.91, CI: 0.83–0.96). Annual variation in detection probability was not correlated with maximum summer temperatures (Kendall's $\tau = 0.36$, $P = 0.14$), minimum winter temperatures (Kendall's $\tau = -0.36$, $P = 0.14$), or total winter precipitation (Kendall's $\tau = -0.14$, $P = 0.72$).

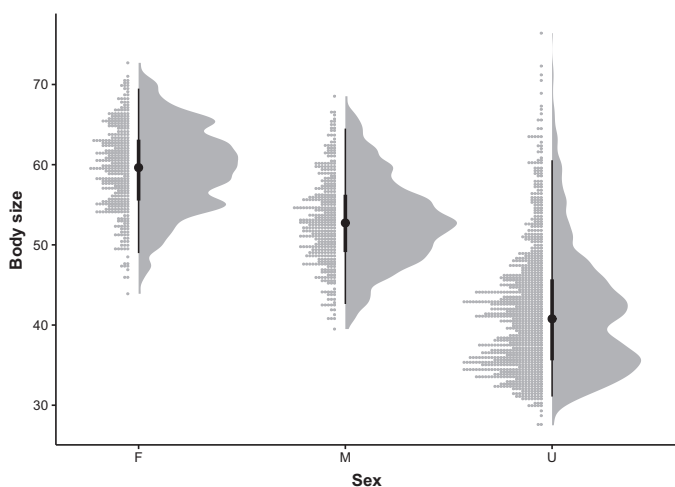


Fig. 2. Body size distributions for males (M), females (F), and individuals of unknown sex (U). Sizes are snout-vent length (SVL) in millimeters. Points represent the raw data points; the center lines show mean, 75%, and 95% confidence intervals; and the shaded region is an approximate density. The average size of females was larger than males ($t = 13.4$, $df = 247$, $P < 0.001$) and individuals of unknown sex ($t = 13.4$, $df = 320$, $P < 0.001$), and the average size of males was larger than individuals of unknown sex ($t = 4.1$, $df = 272$, $P < 0.001$).

However, annual variation in detection rates was correlated with total summer precipitation, whereby detection probabilities of adults in the breeding season were higher in years with low amounts of rainfall in the previous summer (Kendall's $\tau = -0.57$, $P = 0.03$; Fig. 3).

Mean survival of adult salamanders was 0.78 (CI: 0.61–0.89; Supplemental Fig. 1; see Data Accessibility). However, survival rates varied considerably among individuals and across years (Figs. 4, 5). Survival rates were positively correlated to body size in all but two years (Fig. 5; Supplemental Fig. 2; see Data Accessibility). Survival for the smallest individuals in our study (30 mm) averaged 0.56 (CI: 0.36–0.75), whereas survival of the largest individuals (80 mm) averaged 0.87 (CI: 0.75–0.94). Survival rates were not correlated with body size in 2015 where survival was uniformly high across

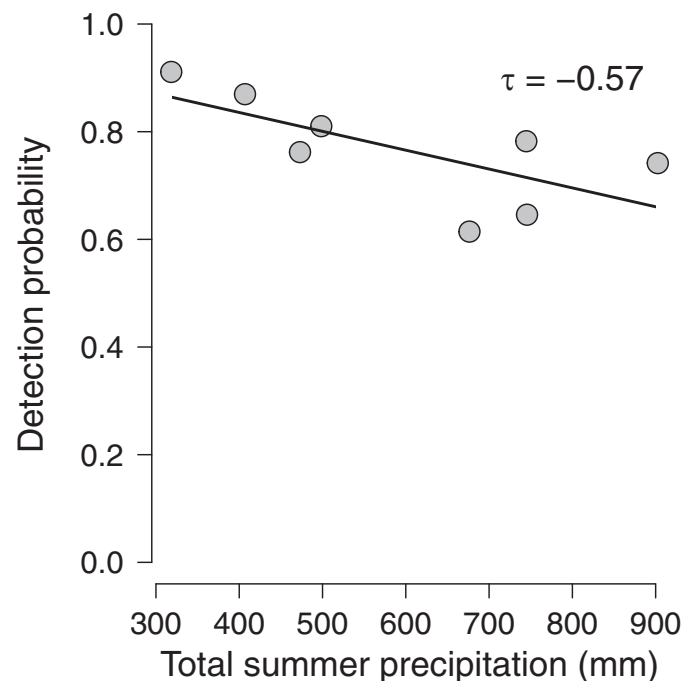


Fig. 3. Detection probability within each breeding season as it relates to rainfall in the previous summer. Kendall's tau was used to determine the strength of the correlation between the variables (Kendall's $\tau = -0.57$, $P = 0.03$). No other correlations were found between environmental conditions and parameters of interest.

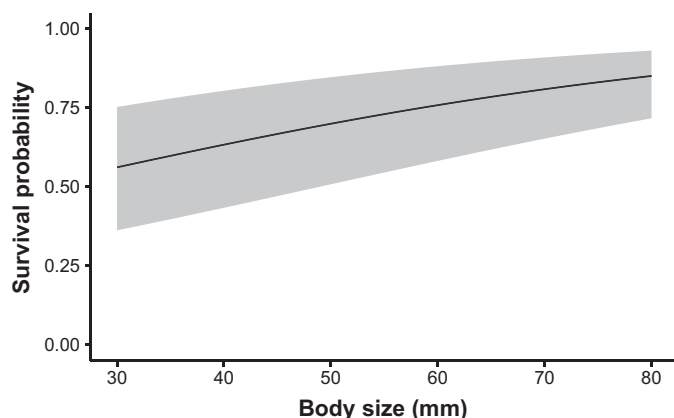


Fig. 4. Size-dependent survival estimates for Reticulated Flatwoods Salamanders averaged across years. Body size reflects snout–vent length (SVL) in mm. The shaded region indicates the 95% credible interval.

individuals and in 2017 where survival was uniformly low across individuals (Fig. 5; Supplemental Fig. 2; see Data Accessibility). Survival was predicted to be highest in 2018 (mean = 0.95, CI: 0.84–0.99) and lowest in 2017 (mean = 0.46, CI: 0.37–0.55). Annual variation in survival was not correlated with maximum summer temperatures (Kendall's $\tau = 0.00$, $P = 0.55$) or minimum winter temperatures (Kendall's $\tau = -0.14$, $P = 0.73$). In addition, annual variation in survival rates was not correlated with total summer precipitation (Kendall's $\tau = -0.07$, $P = 0.64$) or total winter precipitation (Kendall's $\tau = -0.07$, $P = 0.64$).

DISCUSSION

Here we find evidence for a positive relationship between body size and survival in Reticulated Flatwoods Salamanders

and considerable annual variability in adult mortality. Inferring survival rates from incomplete data has been a primary goal of many ecological studies (Pollock et al., 1989; Colchero and Clark, 2012; Gilroy et al., 2012; Gilbert et al., 2014). Conservation practitioners require accurate estimates of survival to parameterize demographic models and quantify extinction risk. Our results provide some insight into the imperiled status of Reticulated Flatwoods Salamanders, carry implications for the long-term viability of populations, and highlight future research directions that will aid ongoing recovery efforts.

The average survival rates estimated for Reticulated Flatwoods Salamanders were similar to those reported for congeners (e.g., Husting, 1965; Trenham et al., 2000; Gamble et al., 2009; Messerman et al., 2020) and align with population trends at the study sites (Brooks et al., 2023). These estimates suggest a mean life expectancy of 3–5 years and a maximum lifespan of 15 years. In support of this finding, a small percentage of individuals marked (as adults) in the first year of the study were recaptured ten years later. Unfortunately, the true age of individuals in this study was not known so the overall demographic structure can only be indirectly inferred. Nevertheless, the apparent longevity of flatwoods salamanders indicates that the terrestrial breeding population acts as a reservoir that is periodically supplemented via sporadic recruitment events (Husting, 1965; Whitford and Vinegar, 1966; Warner and Chesson, 1985; Dodd, 1993; Semlitsch and Bodie, 2003; Harper et al., 2008). In such species, interannual variation in survival has the potential to preclude multiple breeding attempts in a lifetime and may ultimately undermine population viability (Trenham et al., 2000; Griffiths et al., 2010). Improved, non-fatal aging methods offer exciting future avenues for studies that seek to answer such questions in long-lived amphibians (Sinsch, 2015).

The positive correlation we found between body size and survival is unsurprising given the ubiquity of this relationship

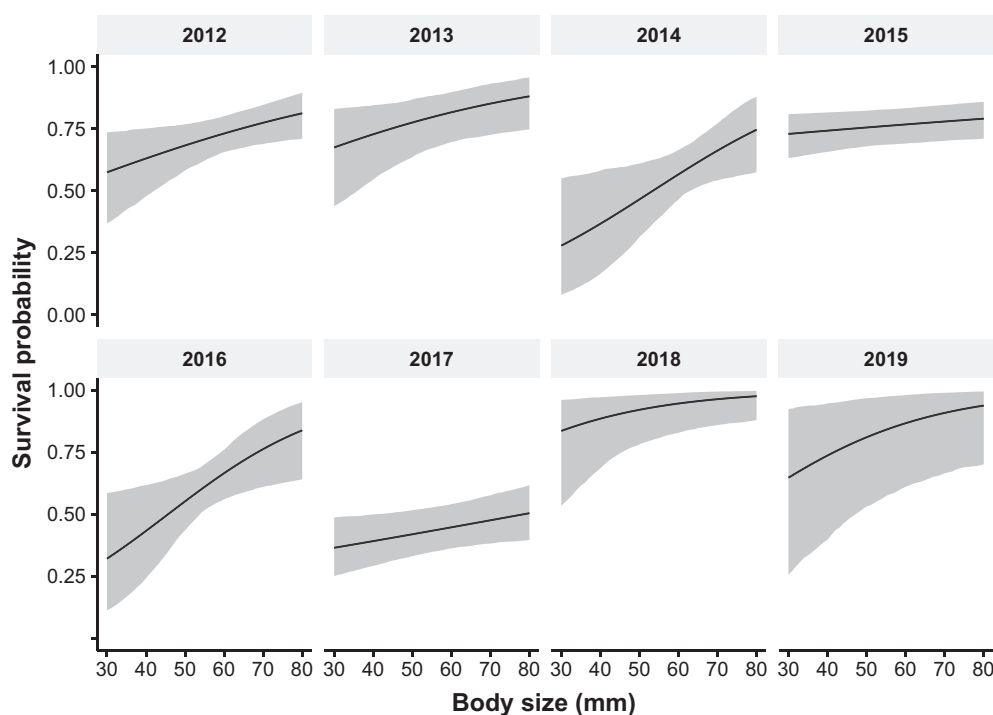


Fig. 5. Size-dependent survival estimates for Reticulated Flatwoods Salamanders by year. Body size reflects snout–vent length (SVL) in mm. The shaded regions indicate the 95% credible intervals.

in nature (Roff, 1992; Cooch, 2002; Ebenman and Persson, 2012). In several amphibians, size at metamorphosis has been shown to have long-term effects on future survival and reproductive success (Semlitsch et al., 1988; De Block and Stoks, 2005; Earl and Whiteman, 2015; Yagi and Green, 2017, 2018). A promising avenue for Reticulated Flatwoods Salamander conservation efforts, therefore, may lie in ensuring high quality habitat conditions for larval growth and development, including fire-maintained herbaceous vegetation, litter sources that provision high quality prey items, and extended wetland hydroperiods (Wilbur and Collins, 1973; Semlitsch et al., 1988; Alvarez and Nicieza, 2002; Altwegg and Reyer, 2003; Richter-Boix et al., 2011; Chandler et al., 2017; Jones et al., 2018; Burrow and Maerz, 2021). In addition, the use of larval headstarting may aid population recovery, when tailored to produce large individuals that have a higher probability of surviving their first summer and returning to breed (Newman, 1998; Griffiths and Pavajeau, 2008; Middleton and Green, 2015). A priority for future research efforts would be to understand the factors that impact size at metamorphosis in Reticulated Flatwoods Salamanders and to what extent larval conditions carry over to impact the terrestrial life stage (Ficetola and Bernardi, 2006; Richter-Boix et al., 2006; Cabrera-Guzmán et al., 2013; Earl and Semlitsch, 2013; Earl and Whiteman, 2015; Yagi and Green, 2018).

Given the strong link between ectothermic life histories and environmental conditions (Laurie and Brown, 1990; Forsman, 1991; Sorci and Clobert, 1999; Kunz and Ekman, 2000), temporal variability in survival rates is considered likely. Several salamander species have been shown to experience a negative energy budget at higher temperatures, resulting in elevated mortality during the hottest summer months (Bobka et al., 1981; Rothermel and Semlitsch, 2006; Homyack et al., 2010, 2011; Rohr and Palmer, 2013). Alternatively, survival of amphibians may be indirectly impacted by temperature through its effect on water balance or prey availability (Spotila, 1972; Maiorana, 1976; Ash et al., 2003; Knapp et al., 2003; Rothermel and Semlitsch, 2006; Tilghman et al., 2012; Messerman et al., 2020). Regardless of the mechanism, there is much concern regarding the impact of climate change on amphibian populations (Means et al., 1996; Blaustein et al., 2001, 2010; Corn, 2005; Lawler et al., 2010; Shoo et al., 2011; Foden et al., 2013; Yiming et al., 2013). However, we found no evidence for coarse metrics of temperature or precipitation being the drivers of variation in survival. Instead we find that detection probabilities, and therefore presumably periods of aboveground activity, are more strongly correlated with environmental conditions. This indicates that despite animals attempting to buffer variation in survival through behavioral means (time spent on the surface), differences in survival rates across years are still pronounced. A key research priority, therefore, is to uncover the proximate factors driving annual variability in survival.

Understanding how survival probabilities change over the course of an individual's life is crucial when scaling up to infer the dynamics of a population. Variability in vital rates can strongly influence a population's vulnerability to local extirpation (Letcher and Horton, 2008; Van de Wolfshaar et al., 2008; Xu et al., 2010). Conservation of pond-breeding amphibians has often neglected the terrestrial phase of the life history (Semlitsch, 2003; Burrow et al., 2021), but there is a growing body of literature demonstrating the sensitivity of amphibian populations to changes in adult survival rates

(Vonesh and De la Cruz, 2002; Harper et al., 2008; Kissel et al., 2020; Terrell et al., 2023). Studies like the one presented here will provide a key component to demographic models that can be used to quantify the threat of extinction in at-risk species. Once the impact of variable survival on the long-term viability of populations has been established, management actions to either dampen or combat that variability can be implemented.

DATA ACCESSIBILITY

All data and code used to perform the analysis are available at <https://github.com/geobro1992/AMBBIS-SURV>. Supplemental material is available at <https://www.ichthyologyandherpetology.org/h2020131>. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

ACKNOWLEDGMENTS

We would like to thank the team of people who have made this research possible. Special mention should be given to Kelly Jones, Brandon Rincon, Steve Goodman, Vivian Porter, and the myriad seasonal technicians involved in data collection. We thank Dylan Childs, Leanna House, Yan Jiao, and Eleni Matechou for their guidance in developing the statistical analyses. We thank the Natural Resources Branch of Eglin Air Force Base (Jackson Guard), the U.S. Fish and Wildlife Service, the Department of Defense Legacy Resource Management Program, the Florida Fish and Wildlife Conservation Commission, the Aquatic Habitat Restoration and Enhancement Program, and the Department of Fish and Wildlife Conservation at Virginia Tech for funding and logistical support on this project. This research was approved by the Virginia Tech Institutional Animal Care and Use Committee, protocol 19-113.

LITERATURE CITED

- Altwegg, R., and H. U. Reyer. 2003. Patterns of natural selection on size at metamorphosis in water frogs. *Evolution* 57:872–882.
- Alvarez, D., and A. G. Nicieza. 2002. Effects of temperature and food quality on anuran larval growth and metamorphosis. *Functional Ecology* 16:640–648.
- Ash, A. N., R. C. Bruce, J. Castanet, and H. Francillon-Vieillot. 2003. Population parameters of *Plethodon metcalfi* on a 10-year-old clearcut and in nearby forest in the southern Blue Ridge Mountains. *Journal of Herpetology* 37:445–453.
- Bailey, L. L., W. L. Kendall, D. R. Church, and H. M. Wilbur. 2004. Estimating survival and breeding probability for pond-breeding amphibians: a modified robust design. *Ecology* 85:2456–2466.
- Barbour, A. B., J. M. Ponciano, and K. Lorenzen. 2013. Apparent survival estimation from continuous mark-recapture/resighting data. *Methods in Ecology and Evolution* 4:846–853.

- 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.
- Blaustein, A. R., L. K. Belden, D. H. Olson, D. M. Green, T. L. Root, and J. M. Kiesecker. 2001. Amphibian breeding and climate change. *Conservation Biology* 15:1804–1809.
- Blaustein, A. R., S. C. Walls, B. A. Bancroft, J. J. Lawler, C. L. Searle, and S. S. Gervasi. 2010. Direct and indirect effects of climate change on amphibian populations. *Diversity* 2:281–313.
- Bobka, M. S., R. G. Jaeger, and D. C. McNaught. 1981. Temperature dependent assimilation efficiencies of two species of terrestrial salamanders. *Copeia* 1981:417–421.
- Brooks, G. C., T. A. Gorman, Y. Jiao, and C. A. Haas. 2020. Reconciling larval and adult sampling methods to model growth across life-stages. *PLoS ONE* 15:e0237737.
- Brooks, G. C., J. A. Smith, T. A. Gorman, and C. A. Haas. 2019. Discerning the environmental drivers of annual migrations in an endangered amphibian. *Copeia* 107:270–276.
- Brooks, G. C., A. Wendt, C. A. Haas, and J. H. Roberts. 2023. Comparing estimates of census and effective population size in an endangered amphibian. *Animal Conservation* 26:839–850.
- Brooks, S. P., E. A. Catchpole, and B. J. Morgan. 2000. Bayesian animal survival estimation. *Statistical Science* 15:357–376.
- Burrow, A. K., B. A. Crawford, and J. C. Maerz. 2021. Ground cover and native ant predation influence survival of metamorphic amphibians in a Southeastern pine savanna undergoing restoration. *Restoration Ecology* 29:e13410.
- Burrow, A. K., and J. C. Maerz. 2021. Experimental confirmation of effects of leaf litter type and light on tadpole performance for two priority amphibians. *Ecosphere* 12:e03729.
- Cabrera-Guzmán, E., M. R. Crossland, G. P. Brown, and R. Shine. 2013. Larger body size at metamorphosis enhances survival, growth and performance of young Cane Toads (*Rhinella marina*). *PLoS ONE* 8:e70121.
- Cayuela, H., R. A. Griffiths, N. Zakaria, J. W. Arntzen, P. Priol, J. P. Léna, A. Besnard, and P. Joly. 2020. Drivers of amphibian population dynamics and asynchrony at local and regional scales. *Journal of Animal Ecology* 89:1350–1364.
- Chandler, H. C., D. L. McLaughlin, T. A. Gorman, K. J. McGuire, J. B. Feaga, and C. A. Haas. 2017. Drying rates of ephemeral wetlands: implications for breeding amphibians. *Wetlands* 37:545–557.
- Chandler, H. C., A. L. Rypel, Y. Jiao, C. A. Haas, and T. A. Gorman. 2016. Hindcasting historical breeding conditions for an endangered salamander in ephemeral wetlands of the southeastern USA: implications of climate change. *PLoS ONE* 11:e0150169.
- Church, D. R., L. L. Bailey, H. M. Wilbur, J. H. Green, and L. Hiby. 2022. Salamander demography at isolated wetlands within mature and regenerating forests. *Diversity* 14:309.
- Colchero, F., and J. S. Clark. 2012. Bayesian inference on age-specific survival for censored and truncated data. *Journal of Animal Ecology* 81:139–149.
- Cooch, E. G. 2002. Fledging size and survival in snow geese: timing is everything (or is it?). *Journal of Applied Statistics* 29:143–162.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
- Corn, P. S. 2005. Climate change and amphibians. *Animal Biodiversity and Conservation* 28:59–67.
- De Block, M., and R. Stoks. 2005. Fitness effects from egg to reproduction: bridging the life history transition. *Ecology* 86:185–197.
- Dodd, C. K., Jr. 1993. Cost of living in an unpredictable environment: the ecology of Striped Newts *Notophthalmus perstriatus* during a prolonged drought. *Copeia* 1993:605–614.
- Duellman, W. E., and L. Trueb. 1994. *Biology of Amphibians*. Johns Hopkins University Press, Baltimore, Maryland.
- Earl, J. E., and R. D. Semlitsch. 2013. Carry-over effects in amphibians: Are characteristics of the larval habitat needed to predict juvenile survival? *Ecological Applications* 23:1429–1442.
- Earl, J. E., and H. H. Whiteman. 2015. Are commonly used fitness predictors accurate? A meta-analysis of amphibian size and age at metamorphosis. *Copeia* 103:297–309.
- Ebenman, B., and L. Persson. 2012. *Size-Structured Populations: Ecology and Evolution*. Springer-Verlag, Berlin, Heidelberg.
- Ergon, T., and B. Gardner. 2014. Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture–recapture data. *Methods in Ecology and Evolution* 5:1327–1336.
- Erwin, K. J., H. C. Chandler, J. G. Palis, T. A. Gorman, and C. A. Haas. 2016. Herpetofaunal communities in ephemeral wetlands embedded within longleaf pine flatwoods of the Gulf Coast plain. *Southeastern Naturalist* 15:431–447.
- Ficetola, G. F., and F. De Bernardi. 2006. Trade-off between larval development rate and post-metamorphic traits in the frog *Rana latastei*. *Evolutionary Ecology* 20:143–158.
- Foden, W. B., S. H. Butchart, S. N. Stuart, J. C. Vié, H. R. Akçakaya, A. Angulo, L. M. DeVantier, A. Gutsche, E. Turak, L. Cao, and S. D. Donner. 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE* 8:e65427.
- Forsman, A. 1991. Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. *Journal of Animal Ecology* 60:253–267.
- Forsman, A. 1996. Body size and net energy gain in gape-limited predators: a model. *Journal of Herpetology* 30:307–319.
- Gamble, L. R., K. McGarigal, D. B. Sigourney, and B. C. Timm. 2009. Survival and breeding frequency in Marbled Salamanders (*Ambystoma opacum*): implications for spatio-temporal population dynamics. *Copeia* 2009:394–407.
- Gilbert, S. L., M. S. Lindberg, K. J. Hundertmark, and D. K. Person. 2014. Dead before detection: addressing the effects of left truncation on survival estimation and ecological inference for neonates. *Methods in Ecology and Evolution* 5:992–1001.
- Gilroy, J. J., T. Virzi, R. L. Boulton, and J. L. Lockwood. 2012. A new approach to the “apparent survival” problem: estimating true survival rates from mark–recapture studies. *Ecology* 93:1509–1516.
- Griffiths, R. A., and L. Pavajeau. 2008. Captive breeding, reintroduction, and the conservation of amphibians. *Conservation Biology* 22:852–861.
- Griffiths, R. A., D. Sewell, and R. S. McCrear. 2010. Dynamics of a declining amphibian metapopulation: survival, dispersal and the impact of climate. *Biological Conservation* 143:485–491.

- Harper, E. B., T. A. Rittenhouse, and R. D. Semlitsch. 2008. Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: predicting extinction risks associated with inadequate size of buffer zones. *Conservation Biology* 22:1205–1215.
- Hegg, D., D. I. MacKenzie, and I. G. Jamieson. 2013. Use of Bayesian population viability analysis to assess multiple management decisions in the recovery programme for the endangered takahe *Porphyrio hochstetteri*. *Oryx* 47:144.
- Homyack, J. A., C. A. Haas, and W. A. Hopkins. 2010. Influence of temperature and body mass on standard metabolic rate of eastern red-backed salamanders (*Plethodon cinereus*). *Journal of Thermal Biology* 35:143–146.
- Homyack, J. A., C. A. Haas, and W. A. Hopkins. 2011. Energetics of surface-active terrestrial salamanders in experimentally harvested forest. *Journal of Wildlife Management* 75:1267–1278.
- Husting, E. L. 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. *Copeia* 1965:352–362.
- Janzen, F. J. 1993. An experimental analysis of natural selection on body size of hatchling turtles. *Ecology* 74:332–341.
- Jolly, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–247.
- Jones, C. N., D. L. McLaughlin, K. Henson, C. A. Haas, and D. A. Kaplan. 2018. From salamanders to greenhouse gases: Does upland management affect wetland function? *Frontiers in Ecology and the Environment* 16:14–19.
- Kellner, K. F., and R. K. Swihart. 2014. Accounting for imperfect detection in ecology: a quantitative review. *PLoS ONE* 9:e111436.
- Kishida, O., G. C. Trussell, K. Nishimura, and T. Ohgushi. 2009. Inducible defenses in prey intensify predator cannibalism. *Ecology* 90:3150–3158.
- Kissel, A. M., S. Tenan, and E. Muths. 2020. Density dependence and adult survival drive dynamics in two high elevation amphibian populations. *Diversity* 12:478.
- Knapp, S. M., C. A. Haas, D. N. Harpole, and R. L. Kirkpatrick. 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. *Conservation Biology* 17:752–762.
- Kunz, C., and J. Ekman. 2000. Genetic and environmental components of growth in nestling blue tits (*Parus caeruleus*). *Journal of Evolutionary Biology* 13:199–212.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* 142:911–927.
- Langrock, R., and R. King. 2013. Maximum likelihood estimation of mark–recapture–recovery models in the presence of continuous covariates. *The Annals of Applied Statistics* 7:1709–1732.
- Laurie, W. A., and D. Brown. 1990. Population biology of marine iguanas (*Amblyrhynchus cristatus*). II. Changes in annual survival rates and the effects of size, sex, age and fecundity in a population crash. *Journal of Animal Ecology* 59:529–544.
- Lawler, J. J., S. L. Shafer, B. A. Bancroft, and A. R. Blaustein. 2010. Projected climate impacts for the amphibians of the Western Hemisphere. *Conservation Biology* 24:38–50.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Letcher, B. H., and G. E. Horton. 2008. Seasonal variation in size-dependent survival of juvenile Atlantic salmon: performance of multistate capture–mark–recapture models. *Canadian Journal of Fisheries and Aquatic Sciences* 65:1649–1666.
- Lind, M. I., F. Persbo, and F. Johansson. 2008. Pool desiccation and developmental thresholds in the common frog, *Rana temporaria*. *Proceedings of the Royal Society B: Biological Science* 275:1073–1080.
- Maiorana, V. C. 1976. Size and environmental predictability for salamanders. *Evolution* 30:599–613.
- Matechou, E., S. Pledger, M. Efford, B. J. T. Morgan, D. L. Thomson, and O. Gimenez. 2013. Estimating age-specific survival when age is unknown: open population capture–recapture models with age structure and heterogeneity. *Methods in Ecology and Evolution* 4:654–664.
- Means, D. B., J. G. Palis, and M. Baggett. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander. *Conservation Biology* 10:426–437.
- Messerman, A. F., R. D. Semlitsch, and M. Leal. 2020. Estimating survival for elusive juvenile pond-breeding salamanders. *The Journal of Wildlife Management* 84:562–575.
- Middleton, J., and D. M. Green. 2015. Adult age-structure variability in an amphibian in relation to population decline. *Herpetologica* 71:190–195.
- Newman, R. A. 1998. Ecological constraints on amphibian metamorphosis: interactions of temperature and larval density with responses to changing food level. *Oecologia* 115:9–16.
- O'Donnell, K. M., and R. D. Semlitsch. 2015. Advancing terrestrial salamander population ecology: the central role of imperfect detection. *Journal of Herpetology* 49:533–540.
- Palis, J. G., M. J. Aresco, and S. Kilpatrick. 2006. Breeding biology of a Florida population of *Ambystoma cingulatum* (Flatwoods Salamander) during a drought. *Southeastern Naturalist* 5:1–8.
- Papadatou, E., R. Pradel, M. Schaub, D. Dolch, H. Geiger, C. Ibañez, G. Kerth, A. Popa-Lisseanu, W. Schorcht, J. Teubner, and O. Gimenez. 2012. Comparing survival among species with imperfect detection using multilevel analysis of mark–recapture data: a case study on bats. *Ecography* 35:153–161.
- Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington and London.
- Pike, D. A., L. Pizzatto, B. A. Pike, and R. Shine. 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology* 89:607–611.
- Pledger, S., K. H. Pollock, and J. L. Norris. 2003. Open capture–recapture models with heterogeneity: I. Cormack–Jolly–Seber model. *Biometrics* 59:786–794.
- Pledger, S., K. H. Pollock, and J. L. Norris. 2010. Open capture–recapture models with heterogeneity: II. Jolly–Seber model. *Biometrics* 66:883–890.
- Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs* 107:3–97.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *The Journal of Wildlife Management* 53:7–15.

- R Core Team.** 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Ramula, S., M. Rees, and Y. M. Buckley.** 2009. Integral projection models perform better for small demographic data sets than matrix population models: a case study of two perennial herbs. *Journal of Applied Ecology* 46:1048–1053.
- Rees, M., and S. P. Ellner.** 2009. Integral projection models for populations in temporally varying environments. *Ecological Monographs* 79:575–594.
- Richter-Boix, A., G. A. Llorente, and A. Montori.** 2006. Effects of phenotypic plasticity on post-metamorphic traits during pre-metamorphic stages in the anuran *Pelodytes punctatus*. *Evolutionary Ecology Research* 8:309–320.
- Richter-Boix, A., M. Tejedo, and E. L. Rezende.** 2011. Evolution and plasticity of anuran larval development in response to desiccation. A comparative analysis. *Ecology and Evolution* 1:15–25.
- Roff, D. A.** 1992. *The Evolution of Life Histories*. Chapman and Hall, New York.
- Rohr, J. R., and B. D. Palmer.** 2013. Climate change, multiple stressors, and the decline of ectotherms. *Conservation Biology* 27:741–751.
- Rose, J. P., G. D. Wylie, M. L. Casazza, and B. J. Halstead.** 2018. Integrating growth and capture–mark–recapture models reveals size-dependent survival in an elusive species. *Ecosphere* 9:e02384.
- Rothermel, B. B., and R. D. Semlitsch.** 2006. Consequences of forest fragmentation for juvenile survival in spotted (*Ambystoma maculatum*) and marbled (*Ambystoma opacum*) salamanders. *Canadian Journal of Zoology* 84:797–807.
- Royle, J. A.** 2008. Modeling individual effects in the Cormack-Jolly-Seber model: a state–space formulation. *Biometrics* 64:364–370.
- Sanchez, K., K. L. Grayson, C. Sutherland, L. M. Thompson, and R. Hernandez-Pacheco.** 2020. Environmental drivers of surface activity in a population of the eastern red-backed salamander (*Plethodon cinereus*). *Herpetological Conservation and Biology* 15:642–651.
- Seber, G. A. F.** 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259.
- Semlitsch, R. D.** 2003. *Amphibian Conservation*. Smithsonian Institution Press, Washington, D.C.
- Semlitsch, R. D., and J. R. Bodie.** 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17:1219–1228.
- Semlitsch, R. D., D. E. Scott, and J. H. Pechmann.** 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology* 69:184–192.
- Shine, R.** 1991. Why do larger snakes eat larger prey items? *Functional Ecology* 5:493–502.
- Shoo, L. P., D. H. Olson, S. K. McMenamin, K. A. Murray, M. Van Sluys, M. A. Donnelly, D. Stratford, J. Terhivuo, A. Merino-Viteri, S. M. Herbert, and P. J. Bishop.** 2011. Engineering a future for amphibians under climate change. *Journal of Applied Ecology* 48:487–492.
- Sinsch, U.** 2015. Skeletochronological assessment of demographic life-history traits in amphibians. *The Herpetological Journal* 25:5–13.
- Sorci, G., and J. Clobert.** 1999. Natural selection on hatchling body size and mass in two environments in the common lizard (*Lacerta vivipara*). *Evolutionary Ecology Research* 1:303–316.
- Spotila, J. R.** 1972. Role of temperature and water in the ecology of lungless salamanders. *Ecological Monographs* 42:95–124.
- Sturtz, S., U. Ligges, and A. Gelman.** 2005. R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software* 12:1–16.
- Su, Y.-R., and J.-L. Wang.** 2012. Modeling left-truncated and right-censored survival data with longitudinal covariates. *The Annals of Statistics* 40:1465–1488.
- 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.
- Terrell, V. C., J. C. Maerz, N. J. Engbrecht, R. M. Stiles, B. A. Crawford, and M. J. Lannoo.** 2023. Breeding population dynamics of threatened crawfish frogs inform targets for habitat management. *Ichthyology & Herpetology* 111:72–86.
- Tilghman, J. M., S. W. Ramee, and D. M. Marsh.** 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. *Biological Conservation* 152:1–9.
- Trenham, P. C., H. B. Shaffer, W. D. Koenig, and M. R. Stromberg.** 2000. Life history and demographic variation in the California tiger salamander (*Ambystoma californiense*). *Copeia* 2000:365–377.
- Tsiatis, A. A., V. DeGruttola, and M. Wulfsohn.** 1995. Modeling the relationship of survival to longitudinal data measured with error: applications to survival and CD4 counts in patients with AIDS. *Journal of the American Statistical Association* 90:23–37.
- USFWS (United States Department of the Interior, Fish and Wildlife Service).** 2009. Endangered and threatened wildlife and plants; Determination of endangered status for Reticulated Flatwoods Salamander; Designation of critical habitat for Frosted Flatwoods Salamander and Reticulated Flatwoods Salamander. *Federal Register* 74:6700–6774.
- USFWS (United States Department of the Interior, Fish and Wildlife Service).** 2020. Species status assessment for the Reticulated Flatwoods Salamander (*Ambystoma bishopi*). USFWS, Panama City, Florida.
- Van de Wolfshaar, K. E., A. M. De Roos, and L. Persson.** 2008. Population feedback after successful invasion leads to ecological suicide in seasonal environments. *Ecology* 89:259–268.
- Von Bertalanffy, L.** 1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology* 10:181–213.
- 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.
- 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.
- Wells, K. D.** 2019. *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago.
- Whitford, W. G., and A. Vinegar.** 1966. Homing, survivorship, and overwintering of larvae in spotted salamanders, *Ambystoma maculatum*. *Copeia* 1966:517–519.
- Wilbur, H. M., and J. P. Collins.** 1973. Ecological aspects of amphibian metamorphosis. *Science* 182:1305–1314.
- Wulfsohn, M. S., and A. A. Tsiatis.** 1997. A joint model for survival and longitudinal data measured with error. *Biometrics* 53:330–339.

- Xu, C. L., B. H. Letcher, and K. H. Nislow. 2010. Size-dependent survival of brook trout *Salvelinus fontinalis* in summer: effects of water temperature and stream flow. *Journal of Fish Biology* 76:2342–2369.
- Yagi, K. T., and D. M. Green. 2017. Performance and movement in relation to postmetamorphic body size in a pond-breeding amphibian. *Journal of Herpetology* 51:482–489.
- Yagi, K. T., and D. M. Green. 2018. Post-metamorphic carry-over effects in a complex life history: behavior and growth at two life stages in an amphibian, *Anaxyrus fowleri*. *Copeia* 106:77–85.
- Yiming, L. I., J. M. Cohen, and J. R. Rohr. 2013. Review and synthesis of the effects of climate change on amphibians. *Integrative Zoology* 8:145–161.