On the use of demographic models to inform amphibian conservation and management: A case study of the Reticulated Flatwoods Salamander

George C. Brooks

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Carola A. Haas, Chair
Thomas A. Gorman
Leanna L. House
Yan Jiao

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ABSTRACT

The Reticulated Flatwoods Salamander, *Ambystoma bishopi*, is an inhabitant of longleaf pine forests in the southeastern United States. Historically distributed across southern Alabama, Georgia, and the Florida panhandle west of the Apalachicola-Flint Rivers, the range of this species has been drastically reduced. It is currently listed as federally endangered under the Endangered Species Act (ESA). Population viability analyses (PVAs) represent a key component of many recovery plans for threatened and endangered species. Here we use 10 years of mark recapture data collected from two breeding populations of *A. bishopi* to construct a demographic model that can be used to evaluate future extinction risk. In chapter one, we quantify population sizes through time, and estimate the impact of annual variability in numbers on genetic viability. This species exists in small (< 500) breeding populations and exhibit annual fluctuations in abundance characteristic of pond-breeding amphibians. In chapter 2, we adopt a modified version of the von Bertalanffy equation to construct size-at-age curves for *A. bishopi* that include the metamorphic transition. Individuals exhibit rapid growth in the larval stage such that they emerge as metamorphs at 60% of their final body size. In chapter 3, we employ a Cormack-Jolly-Seber model, modified to include continuous covariates, to generate size-dependent survival curves. Survival of *A bishopi* exhibits dramatic annual and seasonal variability, but is always positively correlated with body size. Lastly, in chapter 4, we combine the elements of all previous chapters to construct an Integral Projection Model (IPM). Given the prevalence of complete recruitment failure in these populations, and

their relatively small size, extinction probabilities under a business-as-usual model were high. Increasing the frequency of successful recruitment drastically reduces extinction risk; however, adult survival exerts the greatest influence on long-term population growth. To assure the recovery of *A. bishopi*, management must consider all elements of the life-history when allocating resources and effort. More generally, both aquatic and terrestrial habitats must be protected for amphibian conservation to be effective, making them ideal candidates for ‘umbrella species’ status. Amphibian conservation would also benefit from an increase in systematic, long-term data collection.

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GENERAL AUDIENCE ABSTRACT

The southeastern United States is *the* global salamander hotspot, representing a crucible for diversity. Longleaf pine forests, the predominant ecosystem in the southeast, have been reduced to 3% of their former range, with dire consequences for the animals that inhabit them. The Reticulated Flatwoods Salamander, *Ambystoma bishopi*, is endemic to the region, and currently listed as federally endangered owing to recent population declines. A recovery plan for the species therefore, is required by law, under the Endangered Species Act (ESA). A salient component of modern recovery plans are population forecasts that evaluate future extinction risk. Such forecasts can then be used to assess alternative management strategies proposed to improve the species' long-term prospects. By studying two of the last remaining populations of *A. bishopi* from 2010-2019, we were able to collect the data required to construct a demographic model that can be used to run population projections. In some regards, *A. bishopi* is a typical amphibian, in that their populations show dramatic fluctuations in numbers through time, and they exhibit rapid growth in the aquatic larval stage, achieving 60% of their maximum body size in the first three months of life. Flatwoods salamanders breed in ephemeral wetlands, that often dry before successful metamorphosis can occur. The frequency of pond-drying results in a high probability of extinction for a single population, but survival of breeding individuals was equally important when considering long-term persistence. To assure the recovery of *A. bishopi*, management must consider all elements of the life-history when allocating resources and effort. More generally, both aquatic and terrestrial habitats must

be protected for amphibian conservation to be effective, making them ideal candidates for ‘umbrella species’ status.

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To my parents,
for their unwavering love and support

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INTRODUCTION

"I shall let the little I have learnt go forth into the day in order that someone better than I guess the truth, and in his work may prove and rebuke my error. At this I shall rejoice that I was yet a cause whereby such truth has come to light."

Albrecht Dürer (1471-1528)

Amphibian Declines

Global amphibian declines represent one of the biggest crises in conservation biology (Stuart et al. 2004; Wake and Vredenburg, 2008). With at least 2,000 species at risk of extinction (Stuart et al. 2004, González-del-Pliego et al. 2019; IUCN 2019), amphibians are some of the most threatened taxa on earth. Worryingly, another ~2,200 species (~25% of all ~7,900 known species) are data deficient or not evaluated, and thus there is dire need for continued monitoring, assessment, and management of amphibian populations worldwide.

Most amphibians exhibit complex life histories with both larval and adult stages (Duellman and Trueb 1994). Larval periods vary with species, resource availability, and environmental conditions (temperature and precipitation), and can range from 2 weeks to 2 years (Semlitsch 2002). Often, larvae are fully aquatic and invest much of their capital into rapid growth and development prior to metamorphosis, after which they disperse into surrounding terrestrial habitats where they remain until reaching sexual maturity (Madison 1997, Faccio 2003, Semlitsch and Bodie 2003). For many species, adults spend the majority of their lives in terrestrial upland habitat, and many species exhibit a high degree of philopatry, such that most animals return to their natal wetlands to breed (Semlitsch 1998, Semlitsch and Bodie 2003).

Habitat loss is often cited as the primary agent of amphibian declines (Travis 1994, Collins and Storfer 2003, Stuart et al. 2004, Cushman 2006, Sodhi et al. 2008). Globally, wetlands have been diminished by 87% since the 18th century, due to drainage and extraction activities (Davidson 2014, Davidson et al. 2018, Ramsar 2018). In recent decades wetland loss has accelerated to a rate three times that of deforestation, amounting to a 35% loss since the 1970s, with small, isolated wetlands being lost most severely (Davidson 2014, Ramsar 2018). Small, patchily distributed wetlands serve as key amphibian breeding sites, as periodic drying excludes fish predators in most years (Dodd 1992, Semlitsch and Bodie 1998, Gibbons 2003, Gibbons et al. 2006). Many of these wetlands however, are significantly more isolated than historically, and severely degraded by agricultural runoff, herbicide use, disruption to the water table, and the introduction of non-native species (Semlitsch and Bodie 1998, Semlitsch 2002, Collins and Storfer 2003, Stuart et al. 2004, Morton et al. 2006, Davidson 2014, White and Kaplan 2017, Zhu et al. 2017). Increasing isolation and degradation threatens existing metapopulation dynamics in amphibian communities, and ultimately reduces the likelihood of local population persistence (Gibbs 1993, Travis 1994, Hanski et al. 1996, Semlitsch and Bodie 1998, Semlitsch 2002, Greenwald et al. 2009). Despite equivocal evidence for the ubiquity of metapopulations in amphibian taxa (Marsh and Trenham 2001, Smith and Green 2005, Brooks et al. 2019), wetland creation and restoration to promote landscape connectivity are key priorities for amphibian conservation (Semlitsch 2000, Middleton and Green 2015).

Even when aquatic habitats persist on the landscape, loss or degradation of terrestrial habitat can drive amphibian declines and extinctions (Means et al. 1996, Gibbons 2003, Homan et al. 2004, Rubbo & Kiesecker 2005, Schmidt et al. 2005, Harper et al. 2008). There is a growing appreciation for the role that terrestrial adult survival plays in regulating amphibian populations (Biek et al. 2002; Vonesh & De la Cruz 2002); the health of upland forests surrounding breeding wetlands is of fundamental importance to the viability of many amphibian species (Means et al. 1996, Gibbons 2003, Semlitsch and Bodie 2003, Harper et al. 2008). For conservation of pond-breeding amphibians to be effective, management of core upland zones encompassing breeding sites is necessary to support robust adult populations (Means et al. 1996, Semlitsch 1998, Semlitsch 2002, Gibbons 2003, Semlitsch and Bodie 2003, Baldwin et al. 2006, Harper et al. 2008, Greenwald et al. 2009).

Aside from the predominant habitat concerns, amphibians face a suite of additional threats to survival and population persistence, including disease outbreaks, overexploitation, and climate change (Blaustein et al. 1994, 2010, Collins and Storfer 2003, Stuart et al. 2004, Westervelt et al. 2013). Elucidating between the myriad of threats to amphibians can be challenging, as declines are likely driven by a combination of factors operating synergistically, and the relative importance of threats will be specific to region and/or taxa (Semlitsch 2000, 2002, Collins and Storfer 2003, Salice 2012, Semlitsch et al. 2017).

Study System

North America harbors the greatest diversity of salamanders in the world (Petranka 1998). Seven of nine families are represented on the continent, five of which are endemic: Three of the endemic families, Sirenidae, Amphiumidae, and Ambystomatidae, are concentrated in the southeastern United States. Seventy five percent of genera, over half of all described species, occur in the southeastern U.S. (Petranka 1998).

Members of the family Ambystomatidae (colloquially ‘mole salamanders’) are long-lived fossorial animals that breed in ephemeral wetlands, exhibit strong natal philopatry, and often experience boom-and-bust population dynamics (Petranka 1998). Mole salamanders show some of the steepest declines of any amphibian clade (Stuart et al. 2004, Greenwald et al. 2009). Aspects of their life-history, combined with the stochastic nature of their habitat, make this family particularly susceptible to anthropogenic disturbance and extinction (Blaustein et al. 1994, Hanski et al. 1996, Collins and Storfer 2003).

The Reticulated Flatwoods Salamander (Figure 1), *Ambystoma bishopi*, is an inhabitant of longleaf pine forests in the southeastern United States. *Ambystoma bishopi* migrate to and deposit eggs at the edges of ephemeral wetlands between October and December each year. Mature salamanders migrate from upland longleaf pine-wiregrass habitat in which they over-summer, to coincide their arrival with the onset of fall rains that fill breeding wetlands (Anderson and Williamson, 1976, Means et al. 1996, Palis, 1997, Palis et al., 2006, Brooks et al. 2019). Eggs are laid terrestrially and begin embryonic development prior to inundation so as to maximize the time permitted for development before the wetlands dry out in April-May. A delayed hatching strategy is favored when suitable environmental conditions are unpredictable, as with seasonal rainfall (Petranka and Petranka 1981, Martin 1999). If the ponds retain enough water for successful larval development, metamorphs emerge in spring and disperse into upland habitat (Palis, 1995); most breeding adults have already returned to the uplands by this time.

At least some juvenile salamanders have been documented to mature in a single year and thus are capable of breeding after their first summer on land (Palis, 1997, unpublished data). Like other ambystomatids, *A. bishopi* exhibits strong site fidelity, such that the vast majority of individuals will return to their natal wetlands to breed (Palis, 1995, Palis, 1997). This fidelity results in naturally isolated populations partitioned by breeding site, sometimes with microgeographic adaptations to neighboring sites (e.g. Richardson and Urban 2013), however this isolation has likely been exacerbated in recent times with extensive habitat loss and anthropogenic barriers (Gibbs 1993, Waldman and McKinnon 1993, Semlitsch and Bodie 1998, Semlitsch 2002, Gibbons 2003, Bartoszek and Greenwald 2009, Wendt 2017).

Historically distributed across southern Alabama, Georgia, and the Florida panhandle west of the Apalachicola-Flint Rivers, the range of this species has been drastically reduced (Pauly et al., 2007, 2012, Semlitsch et al. 2016). The wholesale reduction of longleaf pine ecosystems constitutes “one of the major social crimes of American history” (Wells and Shunk 1931). Longleaf traditionally served as the habitat matrix surrounding amphibian breeding wetlands, but deforestation, and conversion to slash pine plantations, has led to ecological collapse and the endangerment of species that evolved on these landscapes (Noss et al. 1995, Van Lear et al. 2005, Frost 2007, Hoctor et al. 2007). Longleaf pine now only extends over 3% of its former range (Ware et al. 1993, Van Lear et al. 2005), and it is feared that remnant patches are too small/isolated to support historic floral and faunal communities (Noss et al. 1995, Means 1996, Van Lear et al. 2005, Hoctor et al. 2007).

Longleaf pine communities were historically fire maintained, with burns occurring approximately every 1-3 years in sandhills and wiregrass savannas, every 4-8 years in mesic flatwoods, and every 7-25 years for ephemeral wetland basins (Specht 1979, Frost 1995, Van Lear et al. 2005). Decades of fire-suppression have resulted in a marked deterioration of remaining salamander habitat (Means 1996, Frost 2007). Frequent fires are necessary to stimulate seed germination, prevent woody growth, and reduce duff and fuel load (Means 1996, Van Lear et al. 2005, Frost 2007, Hoctor et al. 2007). It is also important that summer upland fires travel downhill and penetrate into wetland basins to promote graminaceous vegetation and prevent the accumulation of peat deposits (Means 1996, Van Lear et al. 2005, Hoctor et al. 2007). Indeed, in the absence of fire, a dangerously high fuel load can build up, such that when fire is reintroduced to these systems, it can be detrimental to forest health (Friedlander 1970, Specht 1979).

Climate predictions for the southeastern US foreshadow additional future problems with wetland hydrology. The ephemeral wetlands in which many amphibians (Dodd 1992, Dodd et al. 2006) breed are quickly becoming a poisoned chalice; the lack of fish predators and high productivity in these systems make them an ideal nursery for larval amphibians, but in dry years, water levels recede faster than larval development can occur and commonly result in complete recruitment failure (Semlitsch 1987, Pechmann et al. 1991, Chandler et al. 2016, 2017, Jones et al. 2018). Amphibians that use ephemeral wetlands have evolved to coincide breeding migrations with the onset of rainfall and pond-filling, and larval growth rates that reflect typical hydroperiods

(Blaustein et al. 2001, Paton and Crouch 2002, Corn 2005, Todd et al. 2010). Shifts in climate that lead to phenological mismatches regarding the timing of breeding migrations or render previously occupied sites as uninhabitable could prove disastrous for long-term viability of flatwoods salamander populations (Alford and Richards 1999, Blaustein et al. 2001, Corn 2005, Todd et al. 2010, Walls et al. 2013, Chandler et al. 2016, Brooks et al. 2019).

Both the fire-dependent uplands and the ephemeral wetlands are inherently dynamic systems characterized by extreme interannual variability. The dynamic nature of these habitats has raised obstacles for managers attempting to restore areas to ‘natural’ conditions, and to demographers attempting to discern long-term trends from boom-and-bust population cycles (Pechmann et al. 1991, Pechmann and Wilbur 1994, Green 2003, Salvidio 2009). Nevertheless, such stochasticity must be accounted for, as fluctuations in abundance carry implications for genetic viability and will act to make populations more susceptible to disease outbreaks and other catastrophes (Lande and Barrowclough 1987, Green 2003, Whiteman and Wissinger 2005, Salvidio 2009).

Only two breeding wetlands of *A. bishopi* are currently documented in Georgia, and the species has not been documented in Alabama for over three decades. Even the last bastion of the species, Eglin Air Force Base (hereafter Eglin), Florida, has shown worrying signs of declines in recent years. Over half of the ponds known to be occupied by *A. bishopi* in the 1990s failed to yield individuals during extensive sampling efforts in 2014 (a wet year). Currently, less than 50 known sites range-wide harbor flatwoods salamanders, with “populations” being inferred from either a single isolated pond, or even from the detection of a single individual. *A. bishopi* is listed as federally endangered, and is designated as "vulnerable" on the IUCN red list (USFWS 1999, 2009, 2017, IUCN 2019). The work in presented herein will inform the recovery plan for flatwoods salamanders by providing information on population dynamics and extinction risk that can be used to develop specific recovery criteria.

Data Collection and Analyses

To address gaps in our knowledge of flatwoods salamanders, and permit an assessment of viability of remaining populations, two wetlands on Eglin (Figure 2) were completely encircled with drift fences and funnel traps (see Erwin et al. 2016 for details). The drift fences were constructed from 60 cm tall steel (to resist fire) flashing buried in the sediment approximately 15-20 cm. Funnel traps with dimensions 85 cm x 20 cm were placed flush with the fence and ground at approximately 10 m intervals on both sides of the fence (Gibbons and Semlitsch 1981, Palis 1997).

The mass breeding migrations, to and from wetlands, provide the only opportunities to comprehensively sample *A. bishopi* populations; outside of the breeding season, individuals are too secretive, and populations too diffuse, to detect in any great abundance (Semlitsch and Bodie 2003). We began drift fence operations therefore, to coincide with the onset of the breeding season, typically late October or early November. Once we initiated drift fence operations, in the first several years we checked traps multiple times per night through March if water levels receded and there was no reproduction, or May if the wetlands continued to hold water. In some years, we ceased operations for a week in late December and some weekends due to staffing shortages. After developing a better understanding of phenological patterns in flatwoods salamanders, we ceased operations in December and only started again in spring when the likelihood of detecting outbound individuals rose. Upon capture, we recorded the date and time of capture, and uniquely marked each individual using passive integrated transponder (PIT) tags or visual implant elastomer (VIE). We measured snout-vent length (SVL), total length, and mass of all animals captured at drift fences. Sizes reported for both adults and larvae in the following are always SVL unless otherwise specified. Following marking, animals were released on the opposite side of the fence to which they were caught.

By sampling repeatedly across years, one generates a unique capture history for each marked individual, forming a matrix X in which the binary variable x_(i,j) indicates whether individual i was observed on the j^th capture occasion. Mark-recapture data are some of the most common in studies of wild populations and can be used to infer individual-based estimates of key life-history components, as well as population-level processes (Seber 1982, Pollock 1991, Nichols 1992, Schwarz and Seber 1999, Schmidt et al. 2002, Schofield and Barker 2016). Information gleaned from mark-recapture studies regarding demographic parameters provides the foundation to construct projection models, forecast population trends, and assess population viability (Schwarz and Seber 1999, Beissinger and McCullough 2002, Schmidt et al. 2002).

Here we use 9 years of mark-recapture data to investigate the growth, survival, demography, and population dynamics of flatwoods salamanders. In addition, the growth analyses in Chapter 2 incorporated measurement data from larval flatwoods salamanders, collected using standard dipnet sampling techniques (Bishop et al. 2006, Heyer et al. 1994, Wilkinson 2015) between 2009 and 2017. Synthesizing this information, we constructed a projection model to assess the long-term viability of the species and evaluate alternative management strategies on Eglin Air Force Base.

LITERATURE CITED

Alford, R.A. and Richards, S.J., 1999. Global amphibian declines: a problem in applied ecology. Annual review of Ecology and Systematics, 30:133-165.

Anderson J.D. and Williamson, G.K. 1976. Terrestrial mode of reproduction in *Ambystoma cingulatum*. Herpetologica, 32:214-221.

Baldwin, R.F., Calhoun, A.J. and deMaynadier, P.G. 2006. Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the wood frog *Rana sylvatica*. Journal of Herpetology, 40:442-454.

Bartoszek, J. and Greenwald, K.R. 2009. A population divided: railroad tracks as barriers to gene flow in an isolated population of marbled salamanders (*Ambystoma opacum*). Herpetological Conservation and Biology, 4:191-197.

Beissinger, S.R. and McCullough, D.R. 2002. Population viability analysis. University of Chicago Press.

Bishop, D.C., Palis, J.G., Enge, K.M., Printiss, D.J., and Stevenson, D.J. 2006. Capture rate, body size, and survey recommendations for larval *Ambystoma cingulatum* (flatwoods salamanders). Southeastern Naturalist, 5:9–16.

Blaustein, A.R., Wake, D.B., and Sousa, W.P. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. Conservation biology, 8:60-71.

Blaustein, A.R., Belden, L.K., Olson, D.H., Green, D.M., Root, T.L. and Kiesecker, J.M. 2001. Amphibian breeding and climate change. Conservation Biology, 15:1804-1809.

Blaustein, A.R., Walls, S.C., Bancroft, B.A., Lawler, J.J., Searle, C.L. and Gervasi, S.S. 2010. Direct and indirect effects of climate change on amphibian populations. Diversity, 2:281-313.

Brooks, G.C., Smith, J.A., Frimpong, E.A., Gorman, T.A., Chandler, H.C., and Haas, C.A. 2019a. Indirect connectivity estimates of amphibian breeding wetlands from spatially explicit occupancy models. Aquatic Conservation, 1-11.

Brooks, G.C., Smith, J.A., Gorman, T.A. and Haas, C.A. 2019b. Discerning the environmental drivers of annual migrations in an endangered amphibian. Copeia, 107:270-276.

Caughley, G. 1994. Directions in conservation biology. Journal of animal ecology, 215-244.

Chandler H.C. 2015. The effects of climate change and long-term fire suppression on ephemeral pond communities in the southeastern united states. Masters Thesis.

Chandler H.C., Rypel A.L., Jiao Y., Haas C.A., and Gorman T.A. 2016. Hindcasting historical breeding conditions for an endangered salamander in ephemeral wetlands of the southeastern USA: Implications of climate change. PloS one 11(2).

Chandler, H.C., McLaughlin, D. L., Gorman, T. A., McGuire, K. J., Feaga, J. B., and Haas, C. A. 2017. Drying rates of ephemeral wetlands: Implications for breeding amphibians. Wetlands, 37:545-557.

Collins, J.P. and Storfer, A. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distributions, 9:89-98.

Corn, P.S. 2005. Climate change and amphibians. Animal biodiversity and Conservation, 28:59-67.

Cushman, S.A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological Conservation, 128:231–240.

Davidson, N.C., 2014. How much wetland has the world lost? Long-term and recent trends in global wetland area. Marine and Freshwater Research, 65:934-941.

Davidson, N.C., Fluet-Chouinard, E. and Finlayson, C.M., 2018. Global extent and distribution of wetlands: trends and issues. Marine and Freshwater Research, 69:620-627.

Dodd, C. K. 1992. Biological diversity of a temporary pond herpetofauna in north Florida sandhills. Biodiversity and Conservation, 1:125–142.

Duellman, W.E. and Trueb, L., 1994. Biology of amphibians. JHU press.

Erwin, K.J., Chandler, H.C., Palis, J.G., Gorman, T.A. and Haas, C.A. 2016. Herpetofaunal communities in ephemeral wetlands embedded within longleaf pine flatwoods of the Gulf Coastal Plain. Southeastern Naturalist, 15:431-448.

Faccio, S. 2003. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. Journal of Herpetology, 37:479-489.

Friedlander, C.P. 1960. Heathland Ecology. The Scholarship Series in Biology. London: Heinemann.

Frost, C.C. 1995. Presettlement fire regimes in southeastern marshes, peatlands, and swamps. Proceedings of the 19th tall timbers fire ecology conference: fire in wetlands: a management perspective. Tall Timbers Research Inc., Tallahassee.

Frost, C. 2007. History and future of the longleaf pine ecosystem. In The longleaf pine ecosystem (pp. 9-48). Springer, New York, NY.

Gibbons, J.W. 2003. Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. Wetlands, 23:630-635.

Gibbons, J.W. and Semlitsch, R.D. 1981. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. Brimleyana, 7:16.

Gibbons, J.W., Winne, C.T., Scott, D.E., Willson, J.D., Glaudas, X., Andrews, K.M., Todd, B.D., Fedewa, L.A., Wilkinson, L., Tsaliagos, R.N. and Harper, S.J. 2006. Remarkable amphibian biomass and abundance in an isolated wetland: implications for wetland conservation. Conservation Biology, 20:1457-1465.

Gibbs, J.P. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. Wetlands, 13:25–31.

González-del-Pliego, P., Freckleton, R.P., Edwards, D.P., Koo, M.S., Scheffers, B.R., Pyron, R.A. and Jetz, W. 2019. Phylogenetic and trait-based prediction of extinction risk for data-deficient amphibians. Current Biology, 29:1557-1563.

Greenwald, K.R., Purrenhage, J.L. and Savage, W.K. 2009. Landcover predicts isolation in *Ambystoma* salamanders across region and species. Biological Conservation, 142:2493-2500.

Hanski, I., Moilanen, A. and Gyllenberg, M. 1996. Minimum viable metapopulation size. The American Naturalist, 147:527-541.

Heyer, W.R., Donelly, M.A., McDiarmid, R.W., Hayek, L.A.C., and Foster, M.S. 1994. Measuring and monitoring biological diversity: Standard methods for amphibians. Washington, DC: Smithsonian Institution Press.

Hoctor, T.S., Noss, R.F., Harris, L.D. and Whitney, K.A. 2007. Spatial ecology and restoration of the longleaf pine ecosystem. In The Longleaf Pine Ecosystem (pp. 377-402). Springer, New York, NY.

IUCN. 2019. The IUCN Red List of threatened species. http://www.iucnredlist.org.

Jones, C.N., McLaughlin, D.L., Henson, K., Haas, C.A. and Kaplan, D.A. 2018. From salamanders to greenhouse gases: does upland management affect wetland functions? Frontiers in Ecology and the Environment, 16:14-19.

Lande, R., and Barrowclough, G.E. 1987. Effective population size, genetic variation and their use in population management. (pp. 87-123) in M. E. Soulé, ed. Viable populations for conservation. Cambridge Univ. Press, New York.

Nichols, J.D. 1992. Capture-recapture models. BioScience, 42:94-102.

Madison, D. M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. Journal of Herpetology, 31:542–552.

Maiorana, V.C. 1976. Size and environmental predictability for salamanders. Evolution, 599-613.

Martin, K.L. 1999. Ready and waiting: delayed hatching and extended incubation of anamniotic vertebrate terrestrial eggs. American Zoologist, 39:279-288.

Means, D.B. 1996. Longleaf pine forest: going, going, . . . In Eastern old-growth forest: Prospects for rediscovery and recovery, ed. M. Davis, pp. 210–229. Washington, DC: Island Press.

Means, D.B., Palis, J.G. and Baggett, M. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander. Conservation Biology, 10:426-437.

Middleton, J. and Green, D.M. 2015. Adult age-structure variability in an amphibian in relation to population decline. Herpetologica, 71:190-195.

Morton, R.A., Bernier, J.C. and Barras, J.A. 2006. Evidence of regional subsidence and associated interior wetland loss induced by hydrocarbon production, Gulf Coast region, USA. Environmental Geology, 50:261-274.

Noss, R.F., LaRoe, E.T., and Scott, J.M. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. Biological Report 28. Washington, DC: USDI National Biological Service.

Palis J.G. 1995. Larval growth, development, and metamorphosis of *Ambystoma cingulatum* on the gulf coastal plain of Florida. Florida Scientist, 58:352-358.

Palis J.G. 1997. Breeding migration of *Ambystoma cingulatum* in Florida. Journal of Herpetology, 31:71.

Palis J.G., Aresco, M.J., and Kilpatrick, S. 2006. Breeding biology of a florida population of *Ambystoma cingulatum* (flatwoods salamander) during a drought. Southeastern Naturalist, 5:1-8.

Paton, P.W. and Crouch III, W.B. 2002. Using the phenology of pond-breeding amphibians to develop conservation strategies. Conservation Biology, 16:194-204.

Pauly G.B., Piskurek O., and Shaffer H.B. 2007. Phylogeographic concordance in the southeastern united states: The flatwoods salamander, *Ambystoma cingulatum*, as a test case. Molecular ecology 16:415-429.

Pauly, G.B., Bennett, S.H., Palis, J.G. and Shaffer, H.B. 2012. Conservation and genetics of the frosted flatwoods salamander (*Ambystoma cingulatum*) on the Atlantic coastal plain. Conservation genetics, 13:1-7.

Petranka, J.W., and Petranka, J.G. 1981. On the evolution of nest site selection in the marbled salamander, *Ambystoma opacum*. Copeia, 1981:387-391.

Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press.

Pollock, K.H. 1991. Review papers: modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. Journal of the American Statistical Association, 86:225-238.

Ramsar Convention on Wetlands. 2018. Global wetland outlook: State of the world's wetlands and their services to people. Gland, Switzerland: Ramsar Convention Secretariat.

Richardson, J.L. and Urban, M.C. 2013. Strong selection barriers explain microgeographic adaptation in wild salamander populations. Evolution, 67:1729-1740.

Rubbo, M.J., and Kiesecker , J.M. 2005. Amphibian breeding distribution in an urbanized landscape. Conservation Biology, 19:504–511.

Salice, C.J. 2012. Multiple stressors and amphibians: contributions of adverse health effects and altered hydroperiod to population decline and extinction. Journal of Herpetology, 46:675-681.

Salvidio, S. 2009. Detecting amphibian population cycles: the importance of appropriate statistical analyses. Biological Conservation, 142:455-461.

Schmidt, B.R., Schaub, M. and Anholt, B.R. 2002. Why you should use capture-recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration, overdispersion, and common toads. Amphibia-Reptilia, 23:375–388.

Schmidt, B.R., Feldmann, R. and Schaub, M. 2005. Demographic processes underlying population growth and decline in *Salamandra salamandra*. Conservation biology, 19:1149-1156.

Schofield, M. and Barker, R. 2016. 50-year-old curiosities: ancillarity and inference in capture–recapture models. Statistical Science, 31:161-174.

Schwarz, C.J. and Seber, G.A. 1999. Estimating animal abundance: review III. Statistical Science, 427-456.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters (Vol. 8). Caldwell, New Jersey: Blackburn press.

Semlitsch, R.D. 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. Copeia, 1987:61–69.

Semlitsch, R.D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology, 12:1113–1119.

Semlitsch, R.D. 2000. Principles for management of aquatic breeding amphibians. Journal of Wildlife Management, 64:615–631.

Semlitsch, R.D. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. Conservation biology, 16:619-629.

Semlitsch, R.D., and Bodie, J.R. 1998. Are small, isolated wetlands expendable? Conservation Biology, 12:1129–1133.

Semlitsch, R.D. and Bodie, J.R. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology, 17:1219-1228.

Semlitsch, R.D., Walls, S.C., Barichivich, W.J., and O'Donnell, K.M. 2017. Extinction debt as a driver of amphibian declines: an example with imperiled flatwoods salamanders. Journal of herpetology, 51:12-18.

Sodhi, N.S., Bickford, D., Diesmos, A.C., Lee, T.M., Koh, L.P., Brook, B.W., Sekercioglu, C.H. and Bradshaw, C.J. 2008. Measuring the meltdown: drivers of global amphibian extinction and decline. PloS one, 3(2), p.e1636.

Specht, R.L. 1979. Heathlands and related shrublands of the world. In Ecosystems of the World, Vol. 9A Heathlands and related shrublands descriptive studies.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., and Waller, R.W. 2004. Status and trends of amphibian declines and extinctions worldwide. Science, 306:1783–1786.

Travis, J. 1994. Calibrating our expectations in studying amphibian populations. Herpetologica, 50:104-108.

U.S. Fish and Wildlife Service (USFWS). 1999. Final rule to list the flatwoods salamander as a threatened species. Federal Register, 64:15691–15704.

U.S. Fish and Wildlife Service (USFWS). 2009. Determination of endangered status for reticulated flatwoods salamander. Federal Register, 74:6700–6774.

Van Lear, D.H., Carroll, W.D., Kapeluck, P.R. and Johnson, R. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. Forest Ecology and Management, 211:150-165.

Wake, D.B., and Vredenburg, V.T. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences, 105:11466–11473.

Waldman, B. and McKinnon, J.S. 1993. Inbreeding and outbreeding in fishes, amphibians, and reptiles. pp.250-282 in The natural history of inbreeding and outbreeding: theoretical and empirical perspectives. University of Chicago Press, Chicago.

Walls, S.C., Barichivich, W.J., Brown, M.E., Scott, D.E. and Hossack, B.R. 2013. Influence of drought on salamander occupancy of isolated wetlands on the southeastern coastal plain of the United States. Wetlands, 33:345-354.

Ware, S., Frost, C., and Doerr, P.D. 1993. Southern mixed hardwood forest: The former longleaf pine forest. In Biodiversity of the Southeastern United States: Lowland Terrestrial Communities, eds. W.H. Martin, S.G. Boyce, and A.C. Echternacht, pp. 447–493. New York: John Wiley & Sons.

Wells, B.W., and Shunk, I.V. 1931. The vegetation and habitat factors of the coarser sands of the North Carolina plain: An ecological study. Ecological Monographs, 1:465–521.

Westervelt, J.D., Sperry, J.H., Burton, J.L. and Palis, J.G. 2013. Modeling response of frosted flatwoods salamander populations to historic and predicted climate variables. Ecological modelling, 268:18-24.

White, E. and Kaplan, D. 2017. Restore or retreat? Saltwater intrusion and water management in coastal wetlands. Ecosystem Health and Sustainability, 3:e01258.

Whiteman, H.H., Wissinger, S.A. 2005. Amphibian population cycles and long-term data sets. pp. 177–184 In Amphibian declines: Conservation status of United States species. California University Press, Berkeley.

Wilkinson, J.W. 2015. Amphibian survey and monitoring handbook. Exeter, UK: Pelagic Publishing.

Zhu, J., Sun, G., Li, W., Zhang, Y., Miao, G., Noormets, A., McNulty, S.G., King, J.S., Kumar, M. and Wang, X. 2017. Modeling the potential impacts of climate change on the water table level of selected forested wetlands in the southeastern United States. Hydrology and Earth System Sciences, 21:6289-6305.

Figure 1. Adult form of the Reticulated Flatwoods Salamander, *Ambystoma bishopi*.

Photo credit: K. Jones.

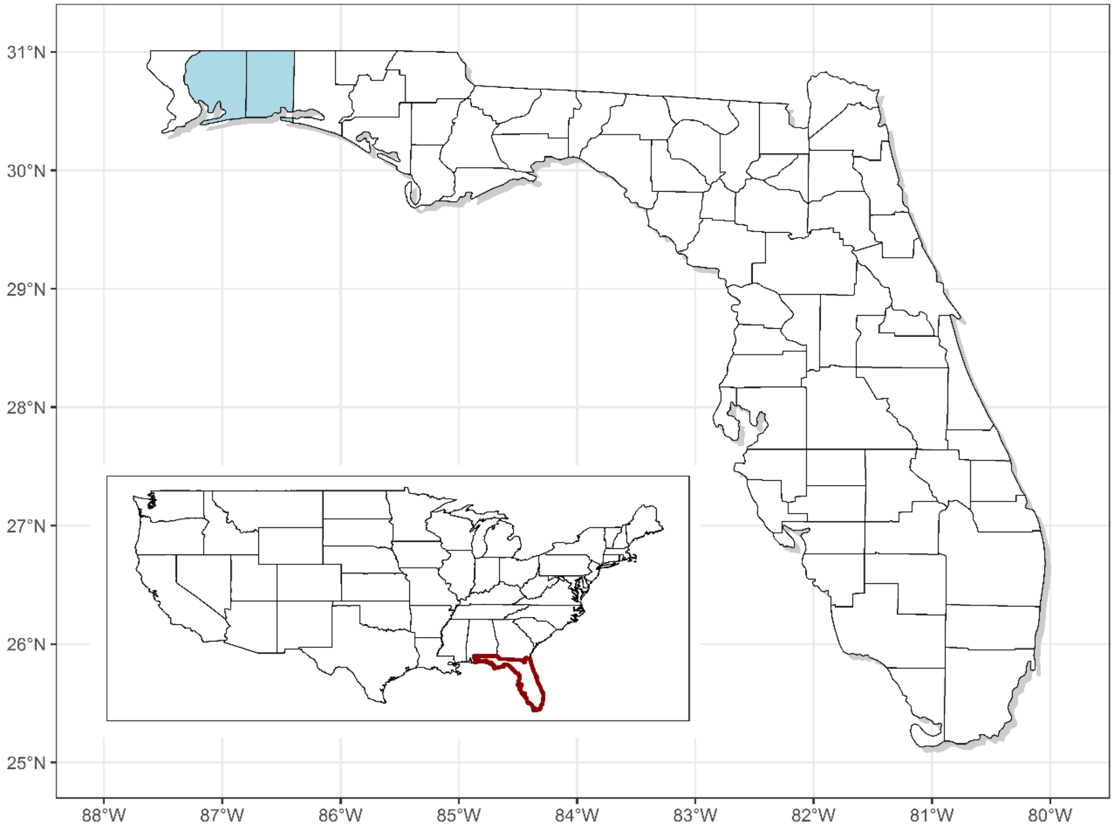

Figure 2. Map depicting study location in the Florida panhandle. Okaloosa and Santa Rosa counties are highlighted.

CHAPTER 1

Population fluctuations and synchronous dynamics in pond-breeding amphibians

ABSTRACT

Reliable estimates of population sizes are of salient importance in applied ecology, and are often used to define recovery goals and assess the efficacy of conservation actions for threatened and endangered species. Long-term viability of populations, however, are more strongly linked to effective population size (N_e) than to raw census size (N). Pond-breeding amphibians typically exhibit large differences between N and N_e due to temporal fluctuations in abundance resulting from stochastic recruitment. Low effective population sizes can be mediated by metapopulation dynamics operating at the landscape scale, however, the evidence for such processes in amphibians is equivocal. Here we investigate population dynamics in breeding wetlands of reticulated flatwoods salamanders, *Ambystoma bishopi*, compare N vs. N_e estimates, and evaluate the assumptions of metapopulation theory in this system. Over the duration of the study, flatwoods salamanders were detected on 229 separate sampling occasions yielding 1785 total captures. Populations exhibited uneven, staggered entry, and recruitment was perfectly synchronized across sites. Fluctuations in population sizes across years produced estimates of N_e that were approximately 80% of average census size, but the stochastic forces that threaten demographic and genetic viability appeared to be offset by the species' longevity. Management actions that seek to dampen temporal fluctuations, either by reducing adult mortality or by achieving more consistent recruitment across years, will reduce extinction risk in these populations. Additionally, managing for a

variety of wetland hydroperiods has the potential to generate asynchronous dynamics between neighboring patches that may serve as a basis for ecological rescue.

INTRODUCTION

Reliable estimates of population sizes are one of the most fundamental and salient metrics in applied ecology (Seber 1982). They are used both to determine whether certain species warrant conservation listing status, and to identify regions that contain substantial proportions of a species' global abundance (Moilanen et al. 2005, Arcos et al. 2012, Ashe et al. 2013, Corrigan et al. 2014, Camaclang et al. 2015). Moreover, population sizes are crucial to ascertain the ecological determinants of scarcity, thereby allowing predictions to be made for species that lack basic descriptive data (Newson et al. 2008). Hence, population estimates often provide one of the first insights that help to direct conservation efforts.

Estimates of population size are frequently used by managers when assessing the efficacy of conservation actions to determine whether recovery goals have been met (Campbell et al. 2002, Morris et al. 2002). Indeed, many recovery plans incorporate the concept of minimum viable populations, MVPs (Soulé, 1987), to provide achievable goals for management and to quantify the biggest sources of risk to populations stemming from the small population paradigm (Caughley, 1994).

The field of conservation however, has shifted focus from recovery criteria based on a population census to those based on 'effective' population size (Soulé 1980, Frankham 1995). The rate of genetic drift within a population is governed not by the raw count of individuals (N) but rather by its effective population size (N_e; Wright 1931). Genetic diversity, and its loss, has been linked with key components of population viability (Allendorf and Leary 1987; Frankham 1995, Newman and Pilson 1997, Bouzat 2010). Furthermore, because the rate of many genetic processes are inversely related to N_e, the genetic effects of a small population are nonlinear, and as such, accurate estimates of N_e are valuable conservation goals (Soulé 1980, Lande and Barrowclough 1987; Nunney and Elam 1994, Kalinowski and Waples 2002, Bouzat 2010, USFWS 2017).

In an "ideal" population, N_e would be equal to raw census size (N), but in most wildlife populations N_e will be <N due to myriad factors including unequal sex ratio, overlapping generations, and variability in reproductive success (Hill 1972, Nunney 1991, Vucetich et al. 1997, Kalinowski and Waples 2002). Unfortunately, methods that account for all influences on N_e have yet to be developed, and thus researchers must choose the factor(s) that presents the most egregious violation from an ideal population (Caballero 1994).

Pond-breeding amphibians exhibit marked stochastic fluctuations in abundance among years (Semlitsch 1983, 1987, Berven 1990, Pechmann et al. 1991, Semlitsch et al. 1996, 2014, Whiteman and Wissinger 2005, Taylor et al. 2006). In the absence of long-term data, it has been challenging to parse out natural fluctuations from population declines in some amphibian taxa (Chesson and Warner 1981, Pechmann et al. 1991, Dodd 1993, Semlitsch et al. 1996, Vucetich and Waite 1998, Alford and Richards 1999, Whiteman and Wissinger 2005, Salvidio 2009). Population fluctuations are thought to exert the greatest influence on N_e and threaten population viability by exacerbating the risk of stochastic extirpation (Wright 1938, Lande and Barrowclough 1987, Caughley 1994, Vucetich et al. 1997, Vucetich and Waite 1998, Whiteman and Wissinger 2005, Salvidio 2009). Populations that fluctuate over time effectively experience repeated bottlenecks followed by recovery, resulting in increased rates of genetic drift (Wright 1938, Lande and Barrowclough 1987, Whitlock 2000). Vucetich and Waite (1998) demonstrated that at least 10 years of data were required to estimate N_e with a reasonable degree of certainty (<10% error), and thus estimates for flatwoods salamanders have hitherto been unattainable. Repeated bottlenecks may expose deleterious alleles to purging events, and therefore reduce inbreeding load (Hedrick 1994, Swindell and Bouzat 2006, Leberg and Firmin 2008; but see Ballou 1997 and Kennedy et al. 2014), but will also act to reduce the adaptive potential of populations to respond to environmental perturbations (Whitlock 2000, Theodorou and Couvet 2006, Bouzat 2010). Quantifying how much genetic diversity is permanently lost from these populations, and the concomitant risk of inbreeding depression, is of pressing concern to support prioritizing management actions.

Management units for aquatic-breeding amphibians often comprise a collection of isolated and discrete habitat patches connected by dispersing individuals. This approach is subject to stochastic events that may result in local extinction and colonization and can be considered synonymous with metapopulations (Hanski 1998, Marsh and Trenham 2001, Smith and Green 2005, Cronin 2006, Frankham et al. 2010). Synchrony in wild populations occurs when spatially isolated patches exhibit similar temporal dynamics (Akçakaya 2000, Liebhold et al. 2004). Three general causes of synchronous dynamics have been proposed: 1) High dispersal between patches (Barbour 1990, Holyoak and Lawler 1996); 2) Similar climatic conditions or other exogenous factors experienced across space and time (the Moran effect; Haydon and Steen 1997, Buonaccorsi et al.

2001); and 3) Trophic interactions such as predator or prey abundance (Bjørnstad et al 1999).

Discerning between these processes when attempting to explain synchrony can be challenging but important for understanding how populations will respond to future environmental perturbations or management actions (Liebhold et al. 2004). The existence of synchrony is particularly important from a conservation standpoint because the degree of synchrony in metapopulations is directly related to the probability of global extinction (Heino et al. 1997). Persistence times for metapopulations decrease as they become more spatially synchronous, and indeed when fully synchronized would cease to function as metapopulations at all (Liebhold et al. 2004).

To shed light on the dynamics of flatwoods salamander populations, and provide a foundation for future demographic modelling efforts, we estimate yearly population sizes, quantify recruitment, and investigate synchrony at two of their last known breeding wetlands. Further, based on annual fluctuations in the numbers of breeding individuals, we derive effective population sizes from our raw census counts to assess the genetic viability of these populations.

METHODS

We fit a hierarchical Bayesian model to 9 years of mark-recapture data from flatwoods salamanders to estimate population sizes and evaluate the degree of synchrony in dynamics of two neighboring wetlands. We adopt the superpopulation parameterization of Crosby and Manley (1985) that uses conditional entry probabilities and an inclusion parameter to account for open populations and zero-inflation in the augmented dataset (Royle and Dorazio 2008, Link and Barker 2010, Kery and Schaub

2013). Each individual in the population is characterized by a unique capture history. Capture histories form a matrix Y in which the binary variable $y_{i,j}$ indicates whether individual i was observed on the j^{th} capture occasion. Site of unobserved individuals is treated as missing data and modelled as Bernoulli variables with a uniform prior in order to estimate the proportion of individuals at each pond.

Each individual carries its own survival history, $z_{i,j}$, a binary character specifying whether individual i was alive or dead on the j^{th} capture occasion (the state process). For the initial capture occasion, z is modelled as a Bernoulli variable with probability $\beta_{s,j}$, where s refers to site, and β represents the entry probability of an individual into the study area, conditional on previous sampling occasions. Thus $\beta_{s,1}$ is simply the likelihood that an individual is already present and available for capture from the outset of the study. For all subsequent occasions, individuals available for capture come from two sources: surviving from the previous sampling occasion, j-1, with probability Φ, and becoming available for capture for the first time with probability $\beta_{s,j}$, conditional on whether a given individual was already present in the study area. Survival was assigned a noninformative beta prior, and entry probabilities are drawn from a Dirichlet distribution, scaled to ensure all probabilities sum to 1.

$$z_{i,1}|\beta_{s,1} \sim Bernoulli(\beta_{s,1})$$

$$z_{i,j}|z_{i,j-1},\dots,z_{i,1},\Phi,\beta_{s,j} \sim Bernoulli(\Phi \times z_{i,j-1} + \beta_{s,j} \times (\prod_{1}^{j-1} 1 - z_{i,j}\ ))$$

$$\beta_{s,j} = \begin{cases} \mu_{s,j}, & j = 1 \\ \dfrac{\mu_{s,j}}{\sum_{1}^{j-1} \mu_{s,j}}, & j > 1 \end{cases}$$

$$\mu_{s,j} = \frac{\alpha_{s,j}}{\sum \alpha_{s,j}}$$

$$\alpha_{s,j} \sim Gamma(1,1)$$

$$\Phi \sim Beta(1,1)$$

To relate the true states of individuals to the observed data, one must include a detection probability to account for individuals not sampled (Kellner and Swihart 2014). Capture histories (observation processes) were modelled as Bernoulli processes with probability of detection p, and probability of inclusion w, such that:

$$y_{i,j} | z_{i,j}, p, w_i \sim Bernoulli(z_{i,j} \times p \times w_i)$$

$$w_i \sim Bernoulli(\Psi)$$

$$\Psi \sim Beta(1,1)$$

$$p \sim Beta(1,1)$$

All models were fitted in R and WinBUGS using Markov chain Monte Carlo optimization (Spiegelhalter et al. 2004, R Core Team 2018). Three chains of MCMC samples were generated from the posterior distributions of the model parameters, each of length 100,000 with the first 10,000 values being discarded as burn-in. To minimize autocorrelation, only every 50th sample was drawn for posterior summaries. Adequate convergence of chains was assessed via potential scale reduction factors $(\hat{R} < 1.1)$. Reported point estimates are posterior medians, with posterior standard deviation in parentheses.

Effective population sizes for the two sites were calculated following Wright (1938). For simplicity, we ignore intergenerational effects, fix the sex ratio at 1:1, and assume reproductive contributions are equal amongst individuals. Here we only consider population fluctuations to influence effective size. In fluctuating populations, genetic stock is disproportionately affected by years experiencing bottlenecks, and it has been shown that N_e approximately equals the harmonic mean of census population sizes (Wright 1938, Caballero 1994, Kalinowski and Waples 2002):

$$N_e = \frac{T}{\sum_{i=1}^{T} \frac{1}{N_i}}$$

Lastly, Pearson's product moment correlation coefficients (PMCC) and a modified version of Kendall's tau (Kendall 1970, Buonaccorsi et al. 2001) were used to quantify levels of synchrony between the two sub-populations. Confidence intervals for both statistics were obtained from bootstrapping over 100,000 draws from the posterior distributions for each population size estimate.

RESULTS

Over the duration of the study, flatwoods salamanders were detected on 229 separate sampling occasions yielding 1785 total captures. Recapture rates differed markedly between individuals, with some individuals captured 13 times and others never recaptured. Despite two opportunities per year to encounter individuals as they move to and from breeding sites, annual detection probabilities were only 0.63 (CI:0.60-0.67). Additionally, over the course of the study, only 2 migration events between the adjacent wetlands were observed.

In line with the known life-history of ambystomatid salamanders, populations exhibited uneven, staggered entry; in some years (2010-11, 14-15) more than 100 individuals became available for capture, whereas no new individuals entered the population in 12-13, 13-14, or 16-17. Estimated population sizes were markedly higher than census counts in all years (Figure 1, Table 2). Estimates of population size were highest in 14-15 following successful recruitment, and lowest in 13-14 following 3 years with no recruitment as a result of inadequate hydroperiods during a drought. Estimates and associated uncertainties for all years are presented in Table 2. Posterior densities for parameters of interest are displayed in Figure 2.

Annual fluctuations at both sites were large enough to reduce estimates of effective population size. Estimates of N_e were approximately 80% of average census size at breeding wetlands (Table 3). A fifth of captured individuals could not be accurately sexed, however equal sex ratios were observed in all but one year. Males outnumbered females by 2:1 at both sites during the 14-15 season following successful recruitment in the previous spring. Lastly, fluctuations in population sizes were highly synchronous between sites (Kendall's tau = 0.79, CI = 0.55 - 0.86, t = 27, p = 0.001; PMCC = 0.95, CI = 0.88 - 0.96, t = 17.96, df = 6, p = 0.001). Both populations exhibited declines in dry years with catastrophic reproductive failures, and rebounded in years with successful recruitment.

DISCUSSION

Complex population dynamics are common in nature (Turchin 2003). Amphibians that breed in ephemeral ponds exhibit drastic variability in recruitment year to year, with successful metamorphosis and recruitment to the adult population depending primarily on hydroperiod and/or recession rate (Semlitsch 1983, 1987, Berven 1990, Pechmann et al. 1991, Dodd 1993, 1995, Semlitsch et al. 2014, Chandler et al. 2017). Catastrophic mortality can occur in years with insufficient precipitation, when pools dry before larvae reach metamorphosis, and the population experiences complete recruitment failure

(Semlitsch 1987, Pechmann et al. 1991, Taylor et al. 2006). Wet years in contrast, can produce dramatic influxes of new recruits and can convey elevated survival rates for breeding adults (Berven 1990, Pechmann et al. 1991, Semlitsch et al. 1996, Taylor et al. 2006, Harper et al. 2008).

Over the course of our study, flatwoods salamander populations fluctuated in number by almost an order of magnitude. As with previous studies, fluctuations were driven by environmental correlates of breeding success (Semlitsch 1987, Berven 1990, Pechmann et al. 1991, Dodd 1993, 1995, Semlitsch et al. 1996, Whiteman and Wissinger 2005, Taylor et al. 2006); estimates of population size were highest in 2015 following the wettest year of the study, and lowest in 2014 following 3 years of drought.

Even large fluctuating populations have an increased likelihood of stochastic extinction (Lande 1993, Green 2003, Hung et al. 2014). In a metapopulation, local extinction can be prevented via rescue effects from neighboring patches, however flatwoods salamanders appear to violate the basic assumptions of metapopulation theory (Hanski et al. 1996, Hanski 1998, 1999). The low connectivity between adjacent wetlands and the near-perfect synchrony in between-patch dynamics suggest that rescue is unlikely to greatly influence patch persistence time (Hanski 1989; Harrison and Quinn 1989; Sutcliffe et al. 2017, but see Sutcliffe et al. 1996). The two wetlands in this study were specifically chosen, owing to their close proximity (~400m apart), to investigate rates of interpatch movement, yet movement events were rarely observed. Thus, although we may see asynchronous dynamics at sites separated by greater distances, it is unlikely that such sites are connected across the landscape (although there is evidence of some connectivity between wetlands separated by up to 1000-1500 m based on occupancy analysis [Brooks et al. 2019] and genetics [Wendt 2017]). Metapopulation dynamics may operate under very particular circumstances, but stochastic forces operating at the site-level will remain a pervasive threat to long-term viability.

Salamanders are long-lived, however, and population fluctuations driven by variable recruitment are partly mediated by the longevity of breeding adults (Taylor et al. 2006, Salvidio 2007, Harper et al. 2008). It could be argued that the drastic variability in abundance of pond-breeding amphibians across years has been overstated as a result of conflating emerging metamorphs with breeding adults. From a viability perspective, it seems more accurate to separate out life-history stages, and focus on trends in the breeding population. As with previous studies of long-lived amphibians (Husting 1965, Whitford & Vinegar 1966, Alford and Richards 1999, Taylor et al. 2006, Harper et al. 2008, but see Palis et al. 2006), no overall decline was observed in adult flatwoods salamanders, despite several catastrophic egg or larval mortality events. Indeed, such populations can only persist on the condition that adults are long-lived enough to survive between breeding bouts, and recruitment in wet years offsets mortality in dry years (Warner and Chesson, 1985, Dodd 1993, Alford and Richards 1999, Taylor et al. 2006, Salvidio 2007). In addition, the rapid maturity previously documented in this species (Palis 1997), and confirmed here (1 year for males, 1-2 years for females), makes it more likely that losses will be offset by gains. Populations that exhibit these life-history strategies are likely to be more sensitive to changes in adult survival than variation in reproductive traits, and thus this knowledge can inform management decisions (Trenham and Shaffer 2005, Harper et al. 2008, Searcy et al. 2015).

Despite the adult population appearing to be somewhat buffered against environmental stochasticity, fluctuations in flatwoods salamander populations across years were substantial enough to reduce effective sizes (Ne) to 80% of censuses. An Ne/N ratio of 0.5 is the theoretical expectation in natural settings (Nunney 1993), but values much lower have been reported for wild populations (Lande and Barrowclough 1987, Frankham 1995, Vucetich et al. 1997, Waples 2002). By failing to account for variation in reproductive success and/or an unequal sex ratio, we have likely overestimated Ne. Genetic estimates of Ne from the same populations support this hypothesis, as they are considerably lower than those obtained here (Wendt 2017), and thus our estimates must be seen as a best-case scenario.

Seminal work in conservation biology concluded that N_e must be >50 to avoid inbreeding depression, and >500 to maintain adaptive potential for long-term viability (Kimura and Ohta 1969, Franklin 1980, Soulé 1980). Recent experimental and theoretical work however, cautions that these thresholds are inadequate to avoid the fixation of deleterious mutations (Newman and Pilson 1997, Frankham et al. 2014). N_e estimates for both populations in this study were ~100-200, suggesting that flatwoods salamanders experience less than 10% inbreeding depression every 5 generations, but are far from the point where long-term adaptive potential is preserved (Franklin 1980, Soulé 1980, Frankham et al. 2014). Once genetic variability has been lost, there is little hope it will be restored. For long-lived vertebrates that experience strong environmental perturbations, evolutionary rescue is predicted to take centuries to come into effect (Vander Wal et al. 2013). Given the precipitous declines seen in many vertebrate clades, and the multiple threats they face, it is likely that species of conservation concern will be extirpated before evolutionary rescue can occur (Edmands 2007, Vander-Wal et al. 2013).

The fluctuations in flatwoods salamander population sizes, typical of many pond-breeding amphibians, carry negative conservation implications (Green 2003, Whiteman and Wissinger 2005, Harper et al. 2008, Salvidio 2009). During prolonged low-density phases, populations are particularly susceptible to demographic and environmental stochasticity, driving local extirpations (Lande 1993, Green 2003, Salvidio 2009, Hung et al. 2014). Further, species that live in changeable environments, and exhibit frequent, local extinctions are especially susceptible to habitat loss and fragmentation (Belovsky 1987, Green 2003, Whiteman and Wissinger 2005, Salvidio 2009). Management actions that seek to dampen temporal fluctuations, either by reducing adult mortality or by achieving more consistent recruitment across years, will reduce extinction risk in these populations. Alternatively, managing for a variety of wetland hydroperiods has the potential to generate asynchronous dynamics between neighboring patches, thereby providing the crucible for ecological rescue. An array of hydrological regimes also acts to maximize beta and gamma diversity in longleaf communities (Semlitsch 2000), and thus should receive more conservation attention than it presently does. Lastly, to improve future prospects for the genetic viability of imperiled amphibians, conservation efforts should seek to retain distinct genotypes and to restore connectivity between artificially isolated populations (Gibbs 2000, Amezaga et al. 2002, Ramsar 2018).

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LITERATURE CITED

Akçakaya, H.R. 2000. Viability analyses with habitat-based metapopulation models. Population Ecology, 42:45-53.

Alford, R.A. and Richards, S.J. 1999. Global amphibian declines: a problem in applied ecology. Annual review of Ecology and Systematics, 30:133-165.

Allendorf, E.W., and Leary, R.E. 1987. Heterozygosity and fitness in natural populations of animals. Pp. 57-76 in M. E. Soulé, ed. Conservation biology. Sinauer, Sunderland, MA.

Alho J.S., Herczeg G., and Merilä J. 2008. Female-biased sex ratios in subarctic common frogs. Journal of Zoology 275:57-63.

Amezaga, J.M., Santamaría, L. and Green, A.J. 2002. Biotic wetland connectivity—supporting a new approach for wetland policy. Acta oecologica, 23:213-222.

Arcos, J.M., Bécares, J., Villero, D., Brotons, L., Rodríguez, B., and Ruiz, A. 2012. Assessing the location and stability of foraging hotspots for pelagic seabirds: an approach to identify marine Important Bird Areas (IBAs) in Spain. Biological Conservation, 156:30-42.

Ashe, E., Wray, J., Picard, C.R. and Williams, R. 2013. Abundance and survival of Pacific humpback whales in a proposed critical habitat area. PloS one, 8:e75228.

Ballou, J.D. 1997. Ancestral inbreeding only minimally affects inbreeding depression in mammalian populations. Journal of Heredity. 88:169–178.

Belovsky, G.E. 1987. Extinction models and mammalian persistence. pp.35-57 in M.E. Soulé (eds) Viable populations for conservation. Cambridge Univ. Press, New York.

Benton, T.G., Lapsley, C.T., and Beckerman, A.P. 2001. Population synchrony and environmental variation: an experimental demonstration. Ecology Letters, 4:236-243.

Berven, K.A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). Ecology, 71:1599-1608.

Bjørnstad, O.N., Ims, R.A., and Lambin, X. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends in Ecology and Evolution, 14:427–432.

Bouzat, J.L. 2010. Conservation genetics of population bottlenecks: the role of chance, selection, and history. Conservation Genetics, 11:463–478.

Brooks, G.C., Smith, J.A., Frimpong, E.A., Gorman, T.A., Chandler, H.C., and Haas, C.A. 2019. Indirect connectivity estimates of amphibian breeding wetlands from spatially explicit occupancy models. Aquatic Conservation: Marine and Freshwater Ecosystems, 29:1815–1825.

Buonaccorsi, J.P., Elkinton, J.S., Evans, S.R., and Liebhold, A.M. 2001. Measuring and testing for spatial synchrony. Ecology, 82:1668–1679.

Caballero, A. 1994. Developments in the prediction of effective population size. Heredity, 73:657.

Camaclang, A.E., Maron, M., Martin, T.G., and Possingham, H.P. 2015. Current practices in the identification of critical habitat for threatened species. Conservation Biology, 29:482-492.

Campbell, S.P., Clark, J.A., Crampton, L.H., Guerry, A.D., Hatch, L.T., Hosseini, P.R., Lawler, J.J., and O'Connor, R.J. 2002. An assessment of monitoring efforts in endangered species recovery plans. Ecological Applications, 12:674-681.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215-244.

Chandler, H.C. 2015. The effects of climate change and long-term fire suppression on ephemeral pond communities in the southeastern united states. Masters Thesis.

Chandler H.C., Rypel A.L., Jiao Y., Haas C.A., and Gorman T.A. 2016 Hindcasting historical breeding conditions for an endangered salamander in ephemeral wetlands of the southeastern USA: Implications of climate change. PloS one, 11:2.

Chesson, P.L., and Warner, R.R. 1981. Environmental variability promotes coexistence in lottery competitive systems. American Naturalist, 117:923-943.

Corrigan, C.M., Ardron, J.A., Comeros-Raynal, M.T., Hoyt, E., Notarbartolo Di Sciara, G., and Carpenter, K.E. 2014. Developing important marine mammal area criteria: learning from ecologically or biologically significant areas and key biodiversity areas. Aquatic Conservation: Marine and Freshwater Ecosystems, 24:166-183.

Cronin, M. 2006. A proposal to eliminate redundant terminology for intra-species groups. Wildlife Society Bulletin, 34:237-241.

Dodd Jr, C.K. 1993. Cost of living in an unpredictable environment: the ecology of striped newts *Notophthalmus perstriatus* during a prolonged drought. Copeia, 605-614.

Dodd Jr, C.K. 1995. The ecology of a sandhills population of the eastern narrow-mouthed toad, *Gastrophryne carolinensis*, during a drought. Bulletin of the Florida Museum of Natural History, 38:11-41.

Edmands, S. 2007. Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. Molecular Ecology, 16:463–475

Frankham, R. 1995. Inbreeding and extinction: a threshold effect. Conservation Biology, 9:792–799.

Frankham, R., Ballou, J.D., and Briscoe, D.A. 2009. Introduction to conservation genetics. Cambridge University Press.

Frankham, R., Bradshaw, C.J., and Brook, B.W. 2014. Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. Biological Conservation, 170:56-63.

Funk W.C., Tallmon D.A., and Allendorf, F.W. 1999. Small effective population size in the long-toed salamander. Molecular Ecology, 8:1633-1640.

Gibbs, J.P. 2000. Wetland loss and biodiversity conservation. Conservation Biology, 14:314-317.

Green, D.M. 2003. The ecology of extinction: population fluctuation and decline in amphibians. Biological Conservation, 111:331-343.

Greenfell, B.T., Wilson, K. Finkenstädt, B.F., Coulson, T.N., Murray, S., Albon, S.D., Pemberton, J.M., Clutton-Brock, T.H., and Crawley, M. J. 1998. Noise and determinism in synchronized sheep dynamics. Nature, 394:674-677.

Grimm A., Gruber B., and Henle K. 2014. Reliability of different mark-recapture methods for population size estimation tested against reference population sizes constructed from field data. PLoS One, 9:e98840.

Hansen, B.B., Grøtan, V., Aanes, R., Sæther, B.E., Stien, A., Fuglei, E., Ims, R.A., Yoccoz, N.G., and Pederson, A.Ø. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the high arctic. Science, 339:313-315.

Hanski, I. 1989. Metapopulation dynamics: does it help to have more of the same? Trends in Ecology and Evolution, 4:113–114.

Hanski, I., and Woiwod, P. 1993. Spatial synchrony in the dynamics of moth and aphid populations. Journal of Animal Ecology, 62:656-668.

Hanski, I., Pakkala, T., Kuussaari, M., and Lei, G. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos, 21-28.

Hanski, I. 1998. Metapopulation dynamics. Nature, 396:41.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press.

Harper, E.B., Rittenhouse, T.A. and Semlitsch, R.D. 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.

Harrison, S., and Quinn, J. F. 1989. Correlated environments and the persistence of metapopulations. Oikos, 56:293–298.

Hayden, D., and Steen, H. 1997. The effects of large- and small-scale random events on the synchrony of metapopulation dynamics: a theoretical analysis. Proceedings of the Royal Society B: Biological Science, 264:1375-1381.

Hedrick, P.W. 1994. Purging inbreeding depression and the probability of extinction: full-sib mating. Heredity, 73:363–372.

Heino, M., Kaitala, V., Ranta, E., and Lindstrom, J. 1997. Synchronous dynamics and rates of extinction in spatially structured populations. Proceedings of the Royal Society B: Biological Science, 264:481–486.

Hill, W.G. 1972. Effective size of populations with overlapping generations. Theoretical Population Biology, 3:278-289.

Hung, C.M., Shaner, P.J.L., Zink, R.M., Liu, W.C., Chu, T.C., Huang, W.S., and Li, S.H. 2014. Drastic population fluctuations explain the rapid extinction of the passenger pigeon. Proceedings of the National Academy of Sciences, 111:10636-10641.

Husting, E.L. 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. Copeia, 352–362.

Jiao, Y., O'Reilly, R., Smith, E., and Orth, D. 2016. Integrating spatial synchrony/asynchrony of population distribution into stock assessment models: a spatial hierarchical Bayesian statistical catch-at-age approach. ICES Journal of Marine Science, 73:1725–1738.

Johst K, and Drechsler, M. 2003. Are spatially correlated or uncorrelated disturbance regimes better for the survival of species? Oikos, 103:449-56.

Kalinowski S.T., and Waples R.S. 2002. Relationship of effective to census size in fluctuating populations. Conservation Biology, 16:129-136.

Kellner, K.F. and Swihart, R.K. 2014. Accounting for imperfect detection in ecology: a quantitative review. PLoS One, 9:e111436.

Kennedy, E.S., Grueber, C.E., Duncan, R.P., and Jamieson, I.G. 2014. Severe inbreeding depression and no evidence of purging in an extremely inbred wild species—the Chatham Island black robin. Evolution, 68:987-995.

Kéry, M., and Schaub, M. 2012. Bayesian population analysis using winbugs: A hierarchical perspective. Boston, Academic Press.

Kimura, M., and Ohta, T. 1969. The average number of generations until fixation of a mutant gene in a population. Genetics, 61:763–771.

Koenig, W.D. 1998. Spatial autocorrelation in California land birds. Conservation Biology, 12:612–620.

Koenig, W.D. 1999. Spatial autocorrelation of ecological phenomena. Trends in Ecology and Evolution, 14:22-26.

Kuparinen A., Alho J.S., Olin M., and Lehtonen H. 2012. Estimation of northern pike population sizes via mark-recapture monitoring. Fisheries Management and Ecology, 19:323-332.

Lande, R., and Barrowclough, G.E. 1987. Effective population size, genetic variation and their use in population management. Pp. 87-123 in M. E. Soulé, ed. Viable populations for conservation. Cambridge Univ. Press, New York.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist, 142:911-927.

Lande, R., Engen, S., and Saether, B.E. 1999. Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. American Naturalist, 154:271–281.

Leberg, P.L., and Firmin, B.D. 2008. Role of inbreeding depression and purging in captive breeding and restoration programmes. Molecular Ecology, 17:334–343.

Liebhold, A., Koenig, W.D., and Bjørnstad, O.N. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology and Evolutionary Systematics, 35:467-490.

Luikart, G., Ryman, N., Tallmon, D.A., Schwartz, M.K., and Allendorf, F.W. 2010. Estimation of census and effective population sizes: The increasing usefulness of DNA-based approaches. Conservation Genetics, 11:355-373.

Marsh, D.M., and Trenham, P.C. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology, 15:40-49.

Massie, T.M., Weithoff, G., Kucklander, N., Gaedke, U., and Blasius, B. 2015. Enhanced Moran effect by spatial variation in environmental autocorrelation. Nature Communications, 6:1–8.

Moilanen, A., Franco, A.M., Early, R.I., Fox, R., Wintle, B., and Thomas, C.D. 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proceedings of the Royal Society B: Biological Sciences, 272:1885-1891.

Morris, W.F., Bloch, P.L., Hudgens, B.R., Moyle, L.C., and Stinchcombe, J.R. 2002. Population viability analysis in endangered species recovery plans: past use and future improvements. Ecological Applications, 12:708-712.

Newman, D., and Pilson, D. 1997. Increased probability of extinction due to decreased genetic effective population size: experimental populations of *Clarkia pulchella*. Evolution, 51:354-362.

Newson, S.E., Evans, K.L., Noble, D.G., Greenwood, J.J.D., and Gaston, K.J. 2008. Use of distance sampling to improve estimates of national population sizes for common and widespread breeding birds in the UK. Journal of Applied Ecology, 45:1330-1338.

Nunney, L. 1991. The influence of age structure and fecundity on effective population size. Procedings of the Royal Society B: Biological Sciences, 246:71-76.

Nunney, L. 1993. The influence of mating system and overlapping generations on effective population size. Evolution, 47:1329–1341.

Nunney, L., and Elam, D.R. 1994. Estimating the effective population size of conserved populations. Conservation Biology, 8:175-184.

Palis, J.G. 1997. Breeding migration of *Ambystoma cingulatum* in Florida. Journal of Herpetology, 31:71.

Palis, J.G., Aresco, M.J., and Kilpatrick, S. 2006. Breeding biology of a Florida population of *Ambystoma cingulatum* (flatwoods salamander) during a drought. Southeastern Naturalist, 5:1-8.

Pauly, G.B., Piskurek, O., and Shaffer, H.B. 2007. Phylogeographic concordance in the southeastern united states: The flatwoods salamander, *Ambystoma cingulatum*, as a test case. Molecular Ecology, 16:415-429.

Pechmann, J.H.K., Scott, D.E., Semlitsch, R.D., Caldwell, J. P., Vitt, L.J., and Gibbons, W. 1991. Declining amphibian populations: The problem of separating human impacts from natural populations. Science, 253:892-895.

Petranka, J.W., Smith, C.K., and Scott, A.F. 2004. Identifying the minimal demographic unit for monitoring pond-breeding amphibians. Ecological Applications, 14:1065-1078.

R CoreTeam. 2018. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Ramsar Convention on Wetlands. 2018. Global wetland outlook: State of the world’s wetlands and their services to people. Gland, Switzerland: Ramsar Convention Secretariat.

Ranta E., Kaitala V., Lindström J., and Linden H. 1995. Synchrony in population dynamics. Proceedings of the Royal Society B: Biological Science, 262:113–18.

Ranta, E., Kaitala, V., Lindström, J., and Helle, E. 1997. The Moran effect and synchrony in population dynamics. Oikos, 78:136–142.

Ranta, E., Kaitala, V. and Lundberg, P. 1998. Population variability in space and time: the dynamics of synchronous populations. Oikos, 83:376–382.

Robert, A. 2009. The effects of spatially correlated perturbations and habitat configuration on metapopulation persistence. Oikos, 118:1590-1600.

Salvidio, S. 2007. Population dynamics and regulation in the cave salamander *Speleomantes strinatii*. Naturwissenschaften, 94:396–400.

Salvidio, S. 2009. Detecting amphibian population cycles: the importance of appropriate statistical analyses. Biological Conservation, 142:455-461.

Searcy, C.A., Snaas, H., and Shaffer, H.B. 2015. Determinants of size at metamorphosis in an endangered amphibian and their projected effects on population stability. Oikos, 124:724-731.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters (Vol. 8). Caldwell, New Jersey: Blackburn Press.

Semlitsch, R.D. 1983. Structure and dynamics of two breeding populations of the eastern tiger salamander, *Ambystoma tigrinum*. Copeia, 608-616.

Semlitsch, R.D. 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. Copeia, 61–69.

Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., and Gibbons, J.W. 1996. Structure and dynamics of an amphibian community. pp.217-248. In Long-term studies of vertebrate communities,

Semlitsch, R.D. 2000. Principles for management of aquatic-breeding amphibians. The Journal of Wildlife Management, 615-631.

Semlitsch, R.D., Anderson, T.L., Osbourn, M.S. and Ousterhout, B.H. 2014. Structure and dynamics of ringed salamander (*Ambystoma annulatum*) populations in Missouri. Herpetologica, 70:14-22.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. BioScience 31:131-134.

Smith, A.M., and Green, M.D. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography, 28:110-128.

Soulé, M.E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. 151–170 in M.E. Soulé and B.A. Wilcox, (eds). Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Soulé M.E. 1987 Viable populations for conservation. Cambridge University Press, New York.

Spiegelhalter, D.J., Thomas, A., Best, N., and Lunn, D. 2004. WinBUGS user manual. Version 1.4.1. Cambridge, UK: MRC Biostatistics Unit.

Sutcliffe, O.L., Thomas, C.D., and Moss, D. 1996. Synchrony and asynchrony in butterfly population dynamics. Journal of Animal Ecology, 65:85–95.

Sutcliffe, O.L., Thomas, C.D., Yates, T.J., and Greatorex-Davies, J.N. 1997. Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. Oecologia, 109:235-241.

Sutherland, C., Elston, D.A., and Lambin, X. 2012. Multi-scale processes in metapopulations: contributions of stage structure, rescue effect, and correlated extinctions. Ecology, 93:2465-2473.

Swindell, W.R., and Bouzat, J.L. 2006. Reduced inbreeding depression due to historical inbreeding in *Drosophila melanogaster*: evidence for purging. Journal of Evolutionary Biology, 19:1257–1264.

Taylor, B.E., Scott, D.E., and Gibbons, J.W. 2006. Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. Conservation Biology, 20:792-801.

Theodorou, K., and Couvet, D. 2006. On the expected relationship between inbreeding, fitness, and extinction. Genetics. Selection and Evolution, 38:371–387.

Trenham, P.C., Koenig, W.D., and Schaffer, H.B. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. Ecology, 82:3519-3530.

Trenham, P.C., Koenig, W.D., Mossman, M. J., Stark, S.L., and Jagger, L.A. 2003. Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. Ecological Applications, 13:1522-1532.

Trenham, P.C., and Shaffer, H.B. 2005. Amphibian upland habitat use and its consequences for population viability. Ecological Applications, 15:1158–1168.

Turchin, P. 2003. Complex population dynamics: A theoretical/ empirical synthesis. Princeton University Press, Princeton.

U.S. Fish and Wildlife Service. 2017. Recovery plan for the central California distinct population segment of the California tiger salamander (*Ambystoma californiense*). U.S. Fish and Wildlife Service, Pacific Southwest Region, Sacramento, California. v + 69pp.

Vander Wal, E., Garant, D., Festa-Bianchet, M., and Pelletier, F. 2013. Evolutionary rescue in vertebrates: evidence, applications and uncertainty. Philosophical Transactions of the Royal Society B: Biological Sciences, 368.

Vucetich, J.A., Waite, T.A., and Nunney, L. 1997. Fluctuating population size and the ratio of effective to census population size. Evolution, 51:2017-2021.

Vucetich, J.A., and Waite, T.A. 1998. Number of censuses required for demographic estimation of effective population size. Conservation Biology, 12:1023-1030.

Wang, I.J., Johnson, J.R., Johnson, B.B., and Shaffer, H.B. 2011. Effective population size is strongly correlated with breeding pond size in the endangered California tiger salamander, *Ambystoma californiense*. Conservation Genetics 12:911-920.

Waples, R.S. 2002. Effective size of fluctuating salmon populations. Genetics, 161:783-791.

Warner, R.R., and Chesson, P.L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. The American Naturalist, 125:769-787.

Wendt, A.S. 2017. A population genetic investigation of the reticulated flatwoods salamander (*Ambystoma bishopi*) on Eglin Air Force Base. Thesis, Georgia Southern University, Statesboro, GA.

Whiteman, H.H., Wissinger, S.A. 2005. Amphibian population cycles and long-term data sets. pp. 177–184 In: Lannoo, M.L. (Ed.), Amphibian declines: Conservation status of United States species. California University Press, Berkeley.

Whitford, W.G., and Vinegar, A. 1966. Homing, survivorship, and overwintering of larvae in spotted salamanders, *Ambystoma maculatum*. Copeia, 1966:517–519.

Whitlock, M.C. 2000. Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. Evolution, 54:1855–1861.

Wright, S. 1931. Evolution in Mendelian populations. Genetics, 16:97–159.

Wright, S. 1938. Size of population and breeding structure in relation to evolution. Science, 87:430–431.

Table 1. Annual population size estimates of reticulated flatwood salamanders at two neighboring wetland sites on Eglin Air Force Base, Florida, showing both the raw counts from drift fence captures and the mark-recapture estimates with 95% credible intervals. (Numbers at Site 2 in 2010-2011 were artificially low because sampling began several weeks later than at Site 1; in all subsequent years both sites had equal sampling effort.)

Season	*Site 1*		*Site 2*	
	Raw	*Est.*	*Raw*	*Est.*
2010-2011	144	223 (201-250)	40	68 (57-80)
2011-2012	114	191 (167-217)	44	75 (64-90)
2012-2013	62	97 (86-108)	29	53 (42-64)
2013-2014	40	61 (54-70)	22	34 (28-43)
2014-2015	144	214 (193-234)	77	134 (117-151)
2015-2016	121	187 (166-211)	58	94 (80-107)
2016-2017	52	86 (74-100)	33	52 (43-64)
2017-2018	74	122 (103-141)	41	71 (58-84)
2018-2019	70	107 (93-121)	39	68 (56-83)

Table 2. Comparison of mean census and effective population sizes for flatwoods salamander breeding wetlands. Numbers in parentheses are 95% credible intervals.

Site	$\bar{N}$	N_e
1	143	119(105-135)
2	72	63(52-75)

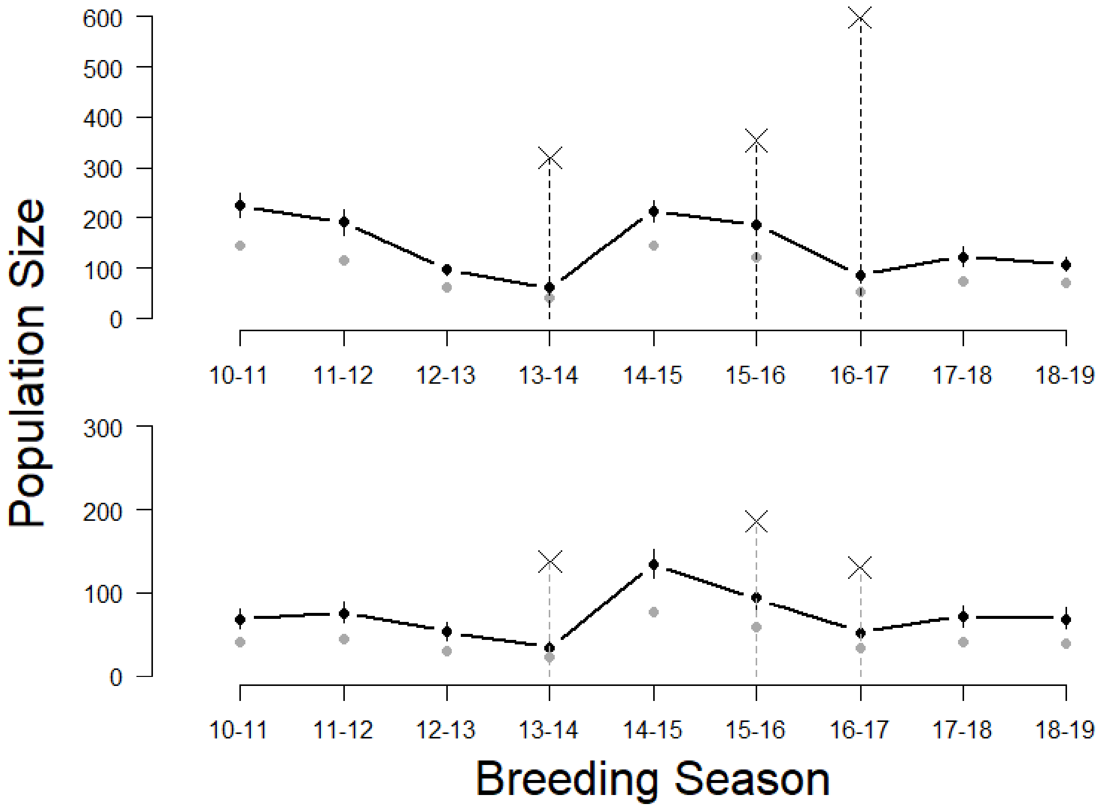

Figure 1. Raw census counts (grey circles) and estimated population sizes (black circles) with 95% credible intervals for two flatwoods salamander breeding wetlands on Eglin Air Force Base, Florida. Years in which wetlands held water long enough for metamorphosis are marked with an X and placed at the point that represents the sum of adult and metamorphs captured each season.

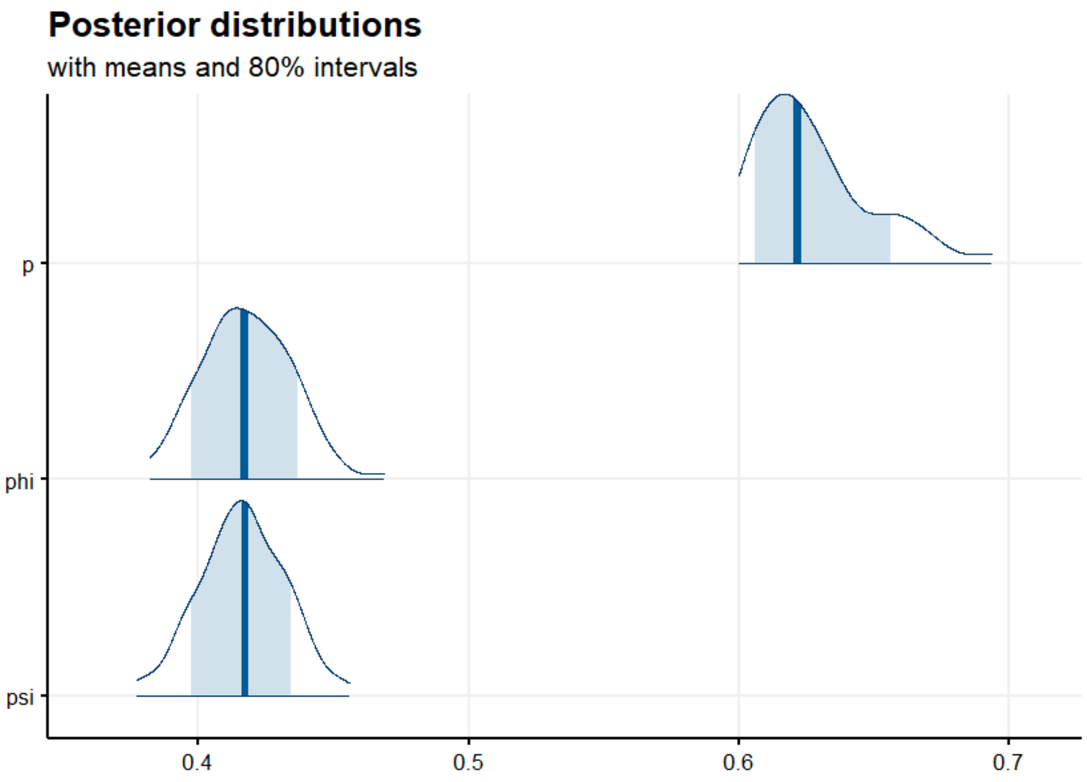

Figure 2. Posterior densities for parameters estimated in the superpopulation model for reticulated flatwoods salamanders at Eglin Air Force Base, where p is detection probability, phi is the inclusion probability and psi represents mean annual survival probability.

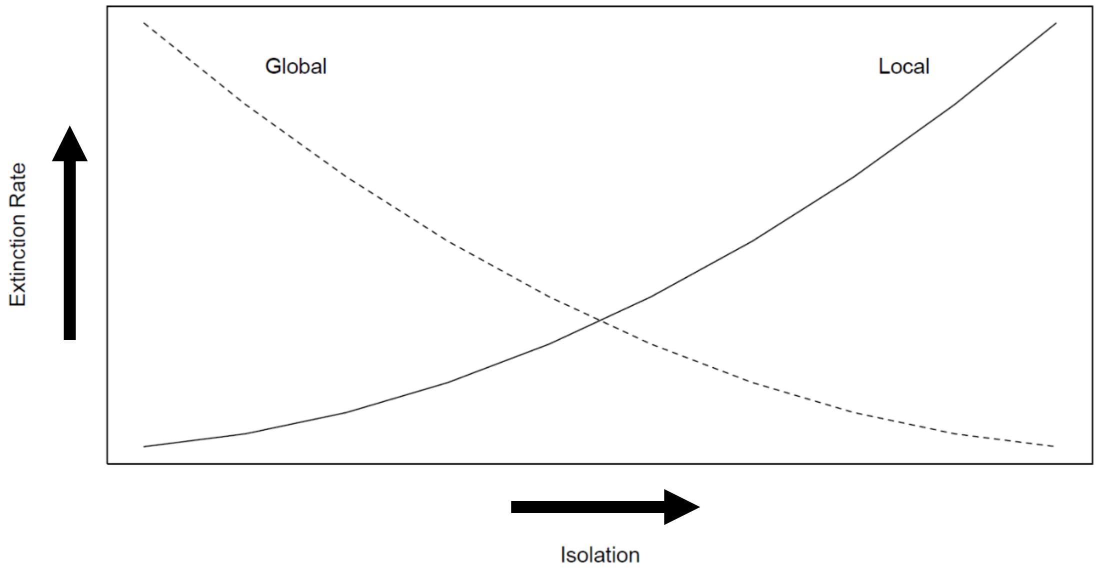

Figure 3. Theoretical expectation of extinction risk given degree of isolation. Local population extinction is predicted to increase exponentially with increasing isolation. Owing to the fact that synchrony in population dynamics is inversely related to isolation, global extinction is predicted to decrease with increasing isolation, as the dynamics of neighboring populations become more asynchronous with distance.

CHAPTER 2

Reconciling larval and adult sampling methods to model growth across amphibian life-stages

ABSTRACT

Individual growth rates are intrinsically related to survival and lifetime reproductive success and, hence, are key determinants of population growth. Efforts to quantify age-size relationships are hampered by difficulties in aging individuals in wild populations. In addition, species with complex life-histories often show distinct shifts in growth that cannot be readily accommodated by traditional modelling techniques. Amphibians are often characterized by rapid larval growth, cessation of growth prior to metamorphosis, and resumption of growth in the adult stage. Compounding issues of non-linear growth, amphibian monitoring programs typically sample larval and adult populations using dissimilar methods. Here we present the first multistage growth model that combines disparate data collected across life-history stages. We model the growth of the endangered Reticulated Flatwoods Salamander, *Ambystoma bishopi*, in a Bayesian framework, that accounts for unknown ages, measurement error, and reconciles dip-net and drift fence sampling designs. Typical of many salamanders, the majority of growth occurs in the larval stage, but the majority of an individual's lifetime is spent as a terrestrial adult. We find evidence for marked variability in growth rate, the timing and age at metamorphosis, and maximum size, within populations. An understanding of growth will contribute to the development of population viability analyses for flatwoods salamanders, will guide management actions, and will ultimately aid the recovery of the species. Our model formulation has broad applicability to amphibians, and likely any

stage-structured organism in which homogenous data cannot be collected across life-stages. The tendency to ignore stage-structure or omit non-conforming data in growth analyses can no longer be afforded given the high stakes of management decisions, particularly for endangered or at-risk populations.

INTRODUCTION

Individual growth rates are intrinsically related to survival and lifetime reproductive success and, hence, are key determinants of population growth (Fenchel 1974, Easterling et al., 2000, Hirst and Forster 2013). Understanding an organism's pattern of growth through time is of paramount importance to evolutionary and ecological studies and is necessary to construct realistic population dynamic models (Quinn & Deriso 1999, Windsland et al. 2013, Maino and Kearney 2015). Without basic demographic and life-history data, projection models and viability analyses used in conservation management are marred with uncertainty (Coulson et al. 2001, Morris and Doak 2002). Furthermore, imprecise growth estimates are likely to bias estimated rates of population growth and extinction probabilities (Quinn & Deriso 1999, McGowan et al. 2011).

If animals can be accurately aged, there are many choices for those wishing to model growth (Quinn & Deriso 1999, Hirst and Forster 2013). Difficulty aging individuals in wild populations however, is a salient problem in ecological studies (Lee 1920, Halliday and Verrell 1988, Cheng and Kuk 2002, Eaton and Link 2011, Hatch and Jiao 2016). Techniques that use physical characteristics (skeletochronology, otoliths, etc.) are often lethal (e.g., Caruso and Rissler 2019), and size-frequency data are highly unreliable, particularly in species with overlapping generations (Eveson et al. 2004). As a result, several models have been modified to estimate growth rates for individuals of unknown age from mark-recapture data (Fabens 1965, Helidoniotis et al. 2011). In the context of endangered species management, mark-recapture studies may offer the only practical method to accurately model growth.

Of the models that have been adapted to mark-recapture data, the von Bertalanffy growth equation (VBGE) has yielded the most applications and model developments aimed at achieving increased biological realism. The VBGE benefits from relatively few model parameters to estimate and can be derived from metabolic theory (von Bertalanffy 1938, West et al. 2001). The VBGE has been modified to include seasonal or inter-annual fluctuations in growth rates (Jiao et al. 2010, Shelton and Mangel 2012), individual heterogeneity within populations (Thomas and Wang 1995, Schofield et al. 2013, Link and Hesed 2015), and shifts in growth as a result of stage-structured life histories (Rogers-Bennett and Rogers 2016).

To date however, modelling shifts in growth requires data collected across life-stages to be homogenous. Whilst this assumption may hold for data collected to detect seasonal trends in growth, this is altogether less common in studies of organisms that exhibit distinct life history stages. In many taxa, life stages are distinct enough to warrant different sampling techniques, and data are often collected piecemeal across an organism’s ontogeny (Eveson et al. 2004, Eaton and Link 2011). Pond breeding amphibians are a case in point. Sampling methods for the aquatic larvae include dipnet and spotlight surveys, whereas terrestrial adults are typically monitored through drift fence studies (Gibbons and Semlitsch 1981, Heyer et al. 1994, Wilkinson 2015). Moreover, many larval amphibians are small enough to preclude unique marking methodologies, or marks may be lost as a result of metamorphosis (Grant 2008). Hence, data collected for larvae and adults are sometimes not only qualitatively, but quantitatively different. Although the two types of data are disparate, they are not independent, and thus growth models can be strengthened by use of a single framework.

Here we model the growth of the federally endangered Reticulated Flatwoods Salamander (hereafter flatwoods salamanders), *Ambystoma bishopi*, using a hierarchical Bayesian approach. Flatwoods salamanders inhabit longleaf pine flatwoods in the southeastern Coastal Plain in the United States. Adults are fossorial and occupy mesic upland habitats, and undertake annual migrations to ephemeral wetlands with well-developed herbaceous groundcover to breed (Palis 1997, Gorman et al. 2009, 2014, Brooks et al. 2019). Flatwoods salamanders lay their eggs in dry wetland basins before they fill, allowing embryos to develop so eggs can hatch when wetlands are inundated (Anderson and Williamson, 1976; Palis, 1997; Gorman et al., 2014). Unpredictable precipitation regimes and pond-filling dates favor such a delayed development strategy (Petranka and Petranka 1981, Martin 1999). Development prior to pond-filling also allows larvae to outgrow potential predators or outcompete potential rivals.

For larval measurements obtained via dipnet surveys, we employ the traditional formulation of the von Bertalanffy equation, using date of pond-filling as an estimate of hatch date (age = 0) for each individual. For terrestrial adults repeatedly sampled at drift fences, we use a modified version of the von Bertalanffy equation that can accommodate mark-recapture information from individuals of unknown age. Additional latent parameters for age and size at metamorphosis permit the two stages to be modelled jointly to estimate a single growth trajectory. The final model incorporates individual heterogeneity in adult growth and measurement error for both length and age data.

Typical of many salamanders, the majority of flatwoods salamander growth occurs in the larval stage, but the majority of an individual’s lifetime is spent as a terrestrial adult. We find evidence for marked variability in growth rate, the timing and age at metamorphosis, and maximum size, within populations. An understanding of growth will contribute to the development of population viability analyses for flatwoods salamanders, will guide management actions, and will ultimately aid the recovery of the species.

MATERIALS AND METHODS

See introduction for details on drift-fence design and mark-recapture protocols for adult salamanders. Larval measurements were obtained through long-term dipnet sampling at all known breeding wetlands across Eglin AFB. Sites were sampled using Model SH-2 and SH-2D (Mid-Lakes Corporation, Knoxville, TN) dipnets and efforts were concentrated in areas with inundated herbaceous vegetation (Bishop et al. 2005, Gorman et al. 2009, Brooks et al. 2019).

We employed a Bayesian hierarchical model to investigate individual growth in flatwoods salamanders. The Bayesian framework accommodates multiple sources of uncertainty and can include prior information regarding parameters of interest (Bacon-Shone 1988, Clark 2004, Shelton and Mangel 2012, Gelman et al. 2013). When growth parameters vary within a population, hierarchical models allow for the estimation of individual-specific growth trajectories whilst still drawing on information from the population as a whole for statistical power (Eaton and Link, 2011). In addition, the hierarchical approach lends itself to inconsistent capture histories prevalent in mark-recapture studies, and can incorporate as much or as little prior knowledge of the organism's biology as deemed appropriate.

MODEL FOR LARVAL STAGE GROWTH

We modelled larval salamander growth using the von Bertalanffy growth equation. The von Bertalanffy equation is most commonly applied in studies of ectothermic vertebrates, but is considered a universal model of growth, and strongly resembles curves derived from basic metabolic principles (West et al. 2001). For a larval individual of age t, the predicted size L_t from the von Bertalanffy equation is expressed as:

$$L_t = L_\infty(1 - e^{k^L(t-t_0)})$$

$$L_\infty \sim U(30, 100)$$

$$t_0 \sim U(-2, 2)$$

$$k^L \sim G(0.1, 0.1)$$

where k^L represents the growth-rate parameter of larval stage individuals, L_∞ the asymptotic size, and t_0 the theoretical age when length = 0. L_∞ was assigned a uniform prior with vague bounds based on the maximum and minimum sizes recorded for the species, k_L was assigned a vague Gamma prior, and t_0 a uniform prior with vague bounds. Following Hatch and Jiao (2016), observed lengths (L_{obs}) are assumed to be drawn from a normal distribution with mean L_t and variance σ_L^2, to account for measurement error. σ_L^2 is assigned a vague gamma prior, and is used across all life-stages in the model:

$$L_{obs}|L_t, \sigma_L^2 \sim N(L_t, \sigma_L^2)$$

$$\sigma_L^2 \sim G(0.1, 0.1)$$

METAMORPHIC TRANSITION

To integrate the larval and adult sub-models, measurements from 766 naturally produced metamorphs were incorporated into the analysis to estimate size and the corresponding age at metamorphosis. Using parameters estimated from the larval model, predicted size at metamorphosis is thus defined:

$$L_{t_m} = L_\infty(1 - e^{k^L(t_m - t_0)})$$

$$t_m \sim U(0.2, 0.7)$$

where t_m is age at metamorphosis. t_m is assigned a uniform prior with bounds based on published data on larval flatwoods salamander developmental rates (Palis 1995).

MODEL FOR ADULT STAGE GROWTH

A modification of the Von Bertalanffy growth equation is necessary to accommodate the unknown ages of adult salamanders and multiple recapture events. For the initial capture occasion, length is modelled similarly to larvae, but with the initial size set to the predicted length at metamorphosis, L_{t_m}:

$$L_t = L_\infty - (L_\infty - L_{t_m})\left(e^{-k^A(t-(t_m+t_0))}\right)$$

$$k^A \sim G(0.1, 0.1)$$

$$t \sim logN(log(\alpha), \sigma_t^2)$$

$$\alpha \sim U(0.3, 20)$$

$$\sigma_t^2 \sim G(2, 0.5)$$

As age of adult individuals at first capture are mostly unknown, they must be estimated and are assumed to be drawn from a truncated lognormal distribution. L_∞ was assigned a uniform prior with vague bounds based on the maximum and minimum sizes recorded for the species, and k^A was assigned a vague Gamma prior. For all subsequent occasions, length-at-age relationships are modelled using the difference in time between capture occasions, δt, such that:

$$L_t = L_\infty - (L_\infty - L_{t_m})\left(e^{k^A((t+\delta t)-(t_m+t_0))}\right)$$

By estimating the unknown age of adults and including parameters for size/age at metamorphosis, the larval, metamorph, and adult data can be reconciled into a single modelling framework and sampled jointly from the posterior. All models were fitted in R and WinBUGS using Markov chain Monte Carlo (MCMC) optimization (Spiegelhalter et al. 2004, R Core Team 2018). Three chains of MCMC samples were generated from the posterior distributions of the model parameters, each of length 500,000 with the first 100,000 values being discarded as burn-in. To minimize autocorrelation, only every 100th sample was drawn for posterior summaries. Adequate convergence was assessed using Gelman-Ruben diagnostics and inspection of trace plots (Gelman et al. 2013). Bayesian p-values were calculated to assess goodness-of-fit (Gelman et al. 2013). All reported point estimates are posterior means, with associate 95% credible intervals in parentheses.

RESULTS

All model parameters adequately converged; all potential scale reductions factors (PSRF) for individual parameters were < 1.1. The multivariate PSRF for the full model was 1.08. Posterior p-values for larval size and adult growth increments both approximated 0.5 (0.51 and 0.506 respectively), indicating a good model fit.

Through dipnet sampling, 411 larval measurements were obtained from 2010 to 2018, between the months of December and April (Figure 1). Larval sizes ranged from 3.9 mm to 42.7 mm SVL. From the three years of drift fence monitoring that produced successful cohorts of recruits (see Chapter 1), 766 metamorphs were captured. Metamorph size ranged from 27.5 mm to 51.9 mm SVL, and shows considerable within- and between-year variability (Figure 2). Across all years of drift-fence monitoring (2010-2018), 927 adult salamanders were captured and marked. Of the adults, 373 were recaptured on at least one occasion, and SVL ranged from 37.5-78.2mm, averaging 58.4mm (Figure 3).

Larvae grew rapidly ($k^L = 1.77; \text{CI: } 1.65 - 1.91$), reaching sizes necessary for metamorphosis within 18 weeks (CI: 15 – 20; Fig 1, 4). Timing and size at metamorphosis were positively correlated (Figure 2) and exhibit marked variability across cohorts. Further, there was some evidence that size at metamorphosis impacted return rates the following year (Figure 3), possibly via reduced survival of smaller metamorphs. Alternatively, smaller metamorphs may take longer to mature, and thus may defer returning to breeding wetlands for several years. Transition between the two parameterizations, from larvae to adult, occurred when individuals averaged 39.3 mm (CI: 37.8 - 40.1; Figure 2, 4). Following metamorphosis, adults grew at an initial growth rate (k^A) of 0.91 (CI: 0.73 – 1.13), corresponding to approximately 6 mm of growth in the first year. Adults grew to an average of 59.0 mm snout-vent length (SVL; CI: 57.9 – 60.0), however there was significant variation among individuals in asymptotic size ($\sigma^2_{L\infty} = 5.0$; Figure 4, 6).

Measurement error and unknown ages of adult individuals contributed the greatest sources of uncertainty. Magnitudes of error in observed lengths sometimes exceeded 5% of the actual measurement, making it difficult to partition out model uncertainty from true variation among individuals. Similarly, discernment of the demographic structure of the population was a challenge given the uncertainty in age estimates. No individual was estimated to be older than 12 years at the study outset (Figure 5), however growth plateaued at approximately 7 years of age, and thus uncertainty in age estimates for older/fully grown individuals was high.

DISCUSSION

Here we present the first multistage growth model that combines disparate data collected across life-history stages. Larval measurements from dipnet/spotlight surveys and mark-recapture data of adults from drift-fence studies were reconciled into a single modeling framework. Estimating growth from only older individuals or failing to accurately quantify uncertainty can severely bias estimates (Lee 1920, Eveson et al. 2007, Hatch and Jiao 2016); the Bayesian approach presented here permits the inclusion of all available data across life-stages whilst accounting for multiple sources of uncertainty in parameters of interest.

Like other ambystomatids, the majority of growth in flatwoods salamanders occurs in the larval stage; individuals reach ~60% of their asymptotic size prior to metamorphosis. Larval growth is an order of magnitude faster than that of adults. Variability in larval growth likely results in only some individuals within a cohort attaining sizes necessary for metamorphosis prior to pond-drying (Wilbur and Collins 1973, Werner 1986). Half of all larval growth trajectories are not steep enough to reach sizes necessary to successfully transition across life-stages (Figure 1). As we did not have repeated measures for larvae however, we were unable to include individual heterogeneity directly into the model parameterization. As such, the high degree of uncertainty in larval growth estimates compared with adults provides only circumstantial evidence for this phenomenon.

Variation in larval growth within a cohort may pale in comparison to variation in size at metamorphosis across years (Figure 2). The distribution of sizes at metamorphosis appears to correspond to the hydroperiod duration in a given year. If wetlands continue to hold water, larvae will postpone metamorphosis in favor of continued growth (Semlitsch 1988). This plasticity in timing holds important consequences for population viability, as increased size at metamorphosis is thought to confer fitness benefits for the remainder of an individual's lifetime (Wilbur and Collins 1973, Semlitsch 1988, Stearns 1992, Scott 1994, Kingsolver and Pfennig 2007, Cabrera-Guzmán et al. 2013, but see Earl and Whiteman 2015). Knowledge of this innate plasticity will prove invaluable to captive rearing efforts, and presents a facet of the life-history that can be targeted by management, through artificial manipulation of pond hydroperiods (Seigel et al. 2006, Shoo et al. 2011).

Following metamorphosis, growth of terrestrial adults slowed considerably and plateaued after approximately 7 years at 60 mm, but was highly variable among individuals. As we were unable to track more than 2-3 individuals across the metamorphic transition, it remains to be seen as to whether variability in adult growth stems from variability in the larval stage, but concomitant individual rates across stages represents the most parsimonious explanation. Flatwoods salamanders are comparatively small for the family Ambystomatidae (Petranka 1998). Metamorphs of congeners regularly exceed 50 mm in snout-vent length (SVL; Petranka 1998), in contrast to the focal species that rarely grew to 45 mm prior to metamorphosis. The diminutive nature of flatwoods salamanders may stem from a shorter larval development time, resulting in smaller individuals at metamorphosis, or owing to their southern latitude.

Our results also suggest flatwoods salamanders are not as long lived as other ambystomatids. No individual was determined to be more than 12 years old. For any species that grows asymptotically, estimating ages for individuals that are at or close to maximum size is challenging, and thus wide confidence intervals on predicted ages of larger individuals prevents any strong conclusions. Survival rates in flatwoods salamanders however, do appear lower than congeners (Chapter 3). It is unclear whether lower longevity reflects a naturally faster life history strategy in flatwoods salamanders compared to closely related species (Stearns 1992), or a sign of inflated mortality that contributes to the imperiled status of the species. Diagnosing the primary agents of mortality in terrestrial individuals is of paramount importance, as it may reveal the cause of declines, and in turn hold the key for species recovery.

Growth and survival of terrestrial individuals exhibit distinct seasonal patterns (unpublished data, A. Liepold, pers. comm., Chapter 3). Growth appears to be negligible during the non-breeding season, and the majority of growth occurs at breeding wetlands. This represents a strong contrast with other salamanders, in which breeding incurs energetic costs, and brooding species must sacrifice foraging opportunities entirely (Gordon 1952, Salthe and Mecham 1974, Maiorana 1976, Kaplan and Crump 1978). If residency at breeding wetlands provides the only opportunity to build up energy resources, this may explain the lack of egg brooding in flatwoods salamanders (Anderson and Williamson 1976, Maiorana 1976). Along similar lines, the faster life-history that flatwoods salamanders appear to exhibit in relation to congeners would favor annual breeding, which would also select against parental care in favor of resource acquisition for next year's clutch. Alternatively, the unpredictability of breeding wetlands may have driven this species to favor a bet-hedging strategy, whereby eggs are laid singly over a large area, to maximize the chances that at least some are inundated and reach the larval stage. This bet-hedging strategy would also prevent loss of entire clutches to fungal pathogens or predators, and provide an opportunity for gravid females to resorb some eggs in dry years (Maiorana 1976). Regardless of the mechanism, a strategy that favors individual egg deposition precludes brooding and frees individuals to forage at breeding wetlands. Evaluating these alternative hypotheses to understand seasonal patterns of growth provides an interesting avenue for future empirical and theoretical work.

Discerning growth rates and size-age relationships can facilitate conservation efforts for threatened and endangered species (Helidoniotis et al. 2011, Armstrong and Brooks 2014). From such metrics, one can derive stable age distribution, age at maturity, and longevity, all of which strongly influence estimates of population growth rates from viability analyses (Caswell 2001). Stage-structured organisms pose a real challenge to this end, and as a result, previous studies are largely limited to species without distinct life-stages (Link and Hesed 2015, Staub 2016, Bendik 2017, Sinsch et al. 2017), or for which homogenous data across stages can be collected (Dortel et al. 2015, Rogers-Bennett and Rogers 2016). For all other circumstances, the tendency is to ignore stage-structure or to omit non-conforming data. We argue however, that for rare taxa, researchers cannot afford these concessions, as even data collected piecemeal contain real ontological insight and utility. Reliable population projections require accurate measures of growth rates across all life stages. Our model formulation has broad applicability to amphibian studies and studies of other stage-structured organisms in which homogenous data cannot be collected across life-stages. Given the ubiquity of complex life-histories and the logistical constraints of monitoring organisms throughout ontogeny, our approach will prove useful for a variety of ecological studies, extending far beyond amphibians. For flatwoods salamanders specifically, an understanding of growth will contribute to the development of population viability analyses, will improve management decisions and actions, and will aid the recovery of the species.

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LITERATURE CITED

Anderson, J.D., and Williamson, G.K. 1976. Terrestrial mode of reproduction in *Ambystoma cingulatum*. Herpetologica, 32:214-221.

Armstrong, D.P., and Brooks, R.J. 2014. Estimating ages of turtles from growth data. Chelonian Conservation and Biology, 13:9-15.

Bacon-Shone, J. 1988. Bayesian methods for growth curves with capture-recapture. Journal of the Royal Statistical Society Series D, 37:307-312.

Bendik, N.F. 2017. Demographics, reproduction, growth, and abundance of Jollyville Plateau salamanders (*Eurycea tonkawae*). Ecology and Evolution, 7:5002:5015.

Brooks, G.C., Smith, J.A., Frimpong, E.A., Gorman, T.A., Chandler, H.C., and Haas, C.A. 2019. Indirect connectivity estimates of amphibian breeding wetlands from spatially explicit occupancy models. Aquatic Conservation: Marine and Freshwater Ecosystems, 29:1815-1825.

Cabrera-Guzmán, E., Crossland, M.R., Brown, G.P., and Shine, R. 2013. Larger body size at metamorphosis enhances survival, growth and performance of young cane toads (*Rhinella marina*). PLoS One, 8:e70121.

Caruso, N.M., and Rissler, L.J. 2019. Museum specimens reveal life history characteristics in *Plethodon montanus*. Copeia, 107:622-631.

Caswell, H. 2001. Matrix population models. construction, analysis and interpretation. Sinauer Associates, Sunderland.

Cheng, Y., and Kuk, A. 2002. Determination of the unknown age at first capture of western rock lobsters (*Panulirus cygnus*) by random effects model. Biometrics, 58:459–462.

Clark, J.S. 2004. Why environmental scientists are becoming Bayesians. Ecology Letters, 8:2-14.

Coulson, T., Mace, G.M., Hudson, E., and Possingham, H. 2001. The use and abuse of population viability analysis. Trends in Ecology and Evolution, 16:219-221.

Dortel, E., Sardenne, F., Bousquet, N., Rivot, E., Million, J., Le Croizierc, G., and Chassot, E. 2015. An integrated Bayesian modeling approach for the growth of Indian Ocean yellowfin tuna. Fisheries Research, 163:69:84.

Earl, J.E., and Whiteman, H.H. 2015. Are commonly used fitness predictors accurate? A meta-analysis of amphibian size and age at metamorphosis. Copeia, 103:297-309.

Eaton, M.J., and Link, W.A. 2011. Estimating age from recapture data: Integrating incremental growth measures with ancillary data to infer age-at-length. Ecological Applications, 21:2487-2497.

Eveson, J.P., Laslett, G.M., and Polacheck, T. 2004. An integrated model for growth incorporating tag-recapture, length-frequency, and direct aging data. Canadian Journal of Fisheries and Aquatic Science, 61:292–306.

Eveson, J., Polacheck, T., and Laslett, G. 2007. Consequences of assuming an incorrect error structure in von Bertalanffy growth models: a simulation study. Canadian Journal of Fisheries and Aquatic Sciences, 64:602–617.

Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth, 29:265–289.

Fenchel, T. 1974. Intrinsic rate of natural increase: the relationship with body size. Oecologica, 14:317-326.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., and Rubin, D.B. 2013. Bayesian data analysis. CRC Press.

Gibbons, J.W., and Semlitsch, R.D. 1981. Terrestrial drift fences with pitfall traps: An effective technique for quantitative sampling of animal populations. Brimleyana, 7:1-6.

Gordon, R.E. 1952. A contribution to the life history and ecology of the plethodontid salamander *Aneides aeneus* (Cope and Packard). American Midland Naturalist, 47:666-701.

Gorman, T.A., Bishop, D.C., and Haas, C.A. 2009. Factors related to occupancy of breeding wetlands by flatwoods salamander larvae. Wetlands, 29:323-329.

Grant, E.H.C. 2008. Visual implant elastomer mark retention through metamorphosis in amphibian larvae. Journal of Wildlife Management, 72:1247-1252.

Halliday, T.R., and Verrell, P.A. 1988. Body size and age in amphibians and reptiles. Journal of Herpetology, 253-265.

Hatch J., and Jiao Y. 2016 A comparison between traditional and measurement-error growth models for weakfish *Cynoscion regalis*. PeerJ, 4:e2431.

Helidoniotis, F., Haddon, M., Tuck, G., and Tarbath, D. 2011. The relative suitability of the von Bertalanffy, Gompertz and inverse logistic models for describing growth in blacklip abalone populations (*Haliotis rubra*) in Tasmania, Australia. Fisheries Research, 112:13-21.

Heyer, W.R., Donelly, M.A., McDiarmid, R.W., Hayek, L.A.C., and Foster, M.S. 1994. Measuring and monitoring biological diversity: Standard methods for amphibians. Washington, Smithsonian Institution Press.

Hirst, A.G., and Forster, J. 2013. When growth models are not universal: evidence from marine invertebrates. Proceedings of the Royal Society B: Biological Science, 280.

Jiao, Y., Rogers-Bennett, L., Taniguchi, I., Butler, J., and Crone, P. 2010 Incorporating temporal variation in the growth of red abalone (*Haliotis rufescens*) using hierarchical Bayesian growth models. Canadian Journal of Fisheries and Aquatic Sciences, 67:730-742.

Kaplan, R.H., and Crump, M.L. 1978. The non-cost of brooding in *Ambystoma opacum*. Copeia, 99-103.

Kingsolver, J.G., and Pfennig, D.W. 2007. Patterns and power of phenotypic selection in nature. Bioscience, 57:561-572.

Lee, R.M. 1920. Age and growth determination in fishes. Nature, 106:49–51.

Link, W.A., and Hesed, K.M. 2015. Individual heterogeneity in growth and age at sexual maturity: A gamma process analysis of capture–mark–recapture data. Journal of Agricultural, Biological, and Environmental Statistics, 20:343-352.

Maino, J.L., and Kearney, M.R. 2015. Testing mechanistic models of growth in insects. Proceedings of the Royal Society B: Biological Science, 282.

Maiorana, V.C. 1976. Size and environmental predictability for salamanders. Evolution, 599-613.

Martin, K.L. 1999. Ready and waiting: delayed hatching and extended incubation of anamniotic vertebrate terrestrial eggs. American Zoologist, 39:279-288.

McGowan, C.P., Runge, M.C., and Larson, M.A. 2011. Incorporating parametric uncertainty into population viability analysis models. Biological Conservation, 144:1400-1408.

Morris, W., and Doak, D. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer Associates, Sunderland.

Palis, J.G. 1995. Larval growth, development, and metamorphosis of *Ambystoma cingulatum* on the Gulf Coastal Plain of Florida. Florida Scientist, 58:352-358.

Petranka, J.W., and Petranka, J.G. 1981. On the evolution of nest site selection in the marbled salamander, *Ambystoma opacum*. Copeia, 387-391.

Quinn, T.J., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

R Core Team. 2018. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rogers-Bennett, L., and Rogers, D. W. 2016. A two-step growth curve: approach to the von Bertalanffy and Gompertz equations. Advances in Pure Mathematics, 6:321-330.

Salthe, S.N., and Mecham, J.S. 1974. Reproductive and courtship patterns. pp.309-521 In B. Lofts (eds), Physiology of the amphibia. Academic Press, New York.

Schofield, M.R., Barker, R.J., and Taylor, P. 2013. Modeling individual specific fish length from capture–recapture data using the von Bertalanffy growth curve. Biometrics, 69:1012-1021.

Scott, D.E. 1994. Effect of larval density on life history traits in *Ambystoma opacum*. Ecology, 75:1383-1396.

Seigel, R.A., Dinsmore, A., and Richter, S.C. 2006. Using well water to increase hydroperiod as a management option for pond-breeding amphibians. Wildlife Society Bulletin, 34:1022–1027.

Semlitsch, R.D., Scott, D.E., and Pechmann, J.H.K. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. Ecology, 69:184-192.

Shelton, A.O., and Mangel, M. 2012. Estimating von Bertalanffy parameters with individual and environmental variations in growth. Journal of Biological Dynamics, 6:3-30.

Shoo, L.P., Olson, D.H., McMenamin, S.K., Murray, K.A., Van Sluys, M., Donnelly, M.A., Stratford, D., Terhivuo, J., Merino-Viteri, A., Herbert, S.M., and Bishop, P.J. 2011. Engineering a future for amphibians under climate change. Journal of Applied Ecology, 48:487-492.

Sinsch, U., Böcking, H., Leskovar, C., Öz, M., and Veith, M. 2017. Demography and lifetime growth patterns in viviparous salamanders (genus *Lyciasalamandra*): Living underground attenuates interspecific variation. Zoologischer Anzeiger, 269:48-56.

Spiegelhalter, D.J., Thomas, A., Best, N., and Lunn, D. 2004. WinBUGS user manual. Version 1.4.1. Cambridge, UK: MRC Biostatistics Unit.

Staub, N.L. 2016. Age, sexual dimorphism, and growth rates in the black salamander, *Aneides flavipunctatus* (Plethodontidae). Copeia, 104:52-59.

Staub, N.L. 2016. The age of plethodontid salamanders: A short review on longevity. Copeia, 104:118-123.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Thomas, M.R., and Wang, Y.G. 1995. Accounting for individual variability in the von Bertalanffy growth model. Canadian Journal of Fisheries and Aquatic Sciences 52:1368-1375.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). Human Biology, 10:181-213.

Werner, E.E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. The American Naturalist, 128:319-341.

West, G.B., Brown, J.H., and Enquist, B.J. 2001. A general model for ontogenetic growth. Nature, 413, 628–31.

Wilbur, H.M., and Collins, J.P. 1973. Ecological aspects of amphibian metamorphosis. Science, 182:1305-1314.

Wilkinson, J.W. 2015 Amphibian survey and monitoring handbook. Pelagic Publishing, Exeter, UK.

Windsland, K., Hvingel, C., Nilssen, E.M., and Sundet, J.H. 2013. Evaluation of von Bertalanffy growth curves for the introduced red king crab (*Paralithodes camtschaticus*) in Norwegian waters. Fisheries Research, 145:15-21.

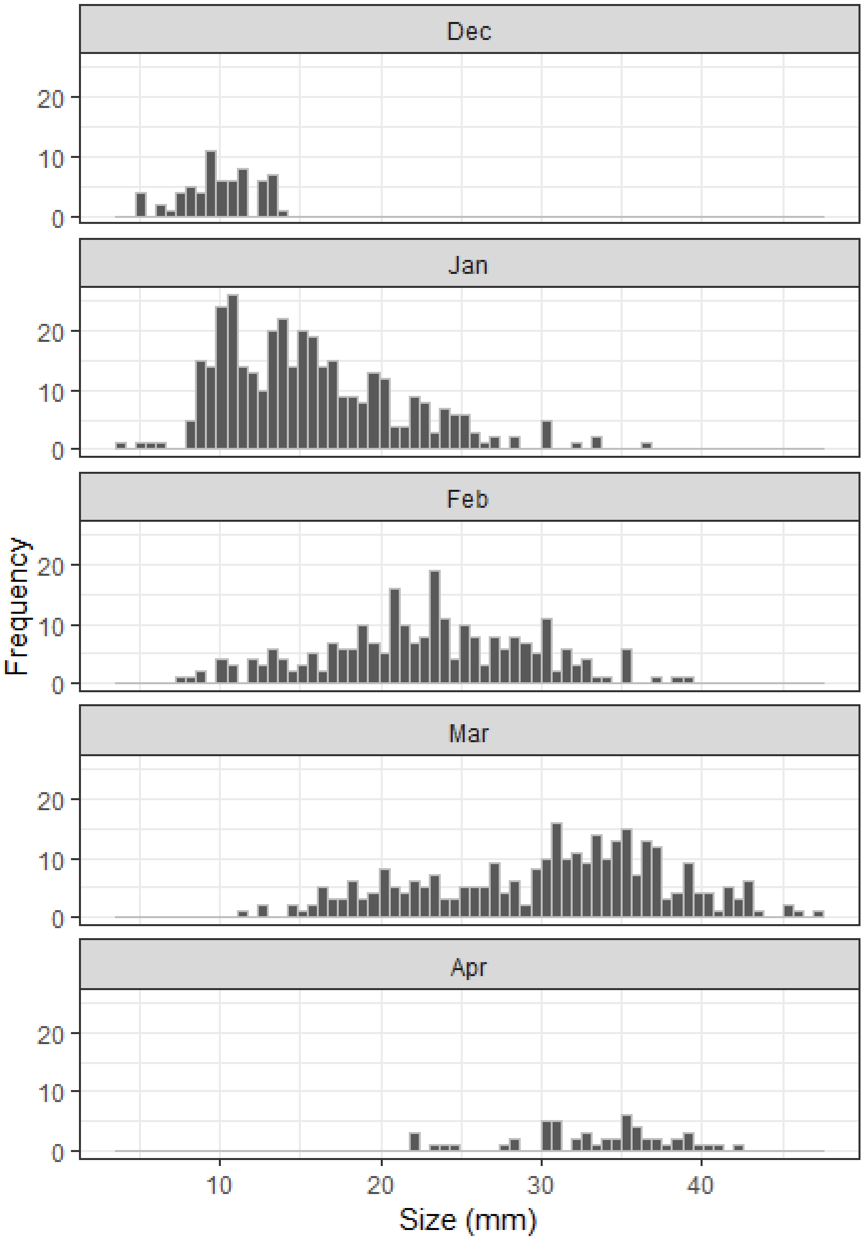

Figure 1. Size distribution of reticulated flatwoods salamander larvae captured by dipnetting and spotlighting at approximately 8-12 wetlands, including the two drift-fenced wetlands, on Eglin Air Force Base, Florida. Measurements are pooled across the years 2010-2018.

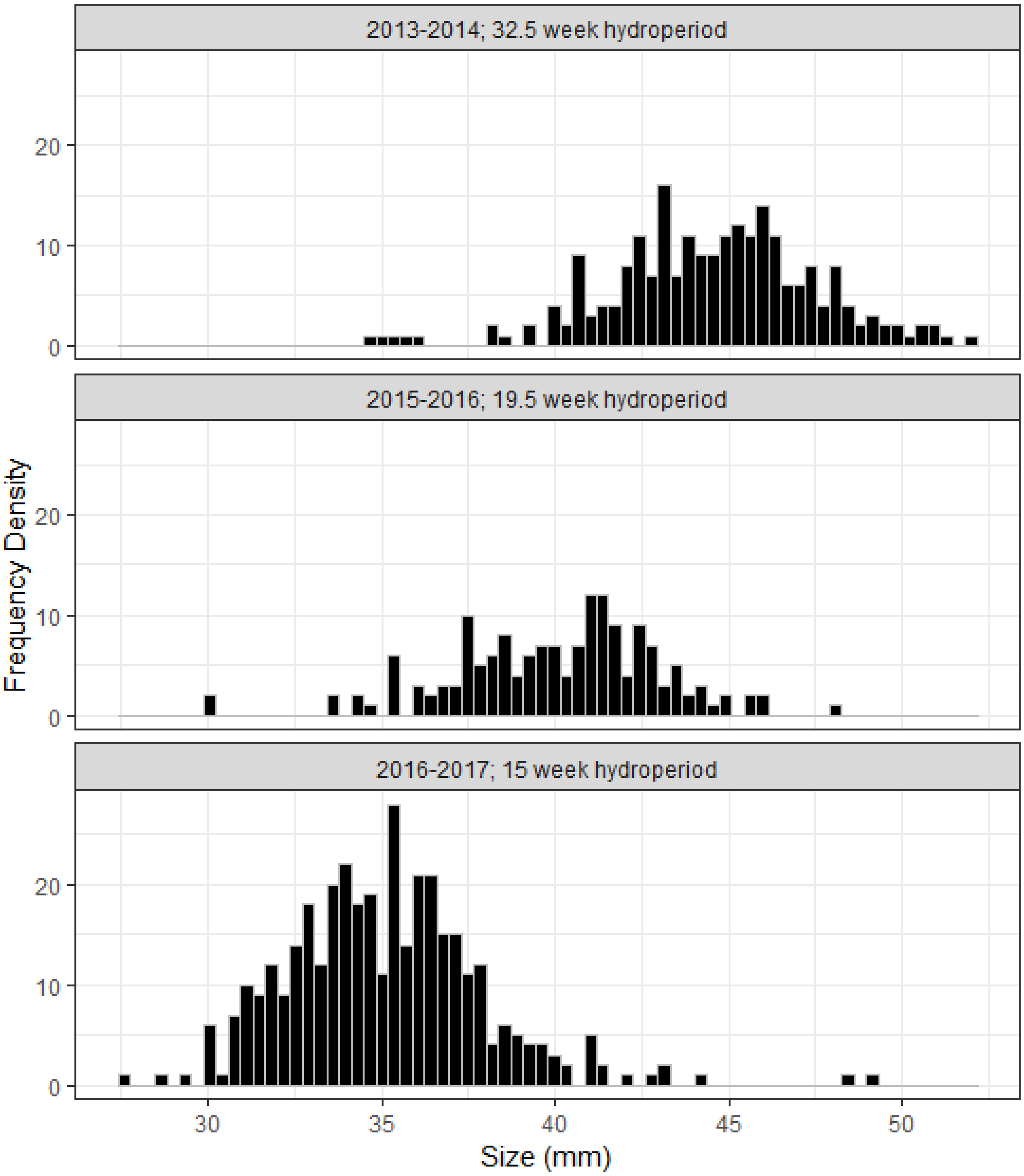

Figure 2. Size distribution of reticulated flatwoods salamander metamorphs captured emigrating from two drift-fenced wetlands on Eglin Air Force Base, Florida, for a subset of years with differing hydroperiods. The year and corresponding hydroperiod for the wetlands that produced these cohorts are displayed above each panel.

Figure 3. Size distribution of reticulated flatwoods salamanders captured as terrestrial forms at two drift-fenced wetlands on Eglin Air Force Base, Florida, across years. Histogram of snout-vent length (SVL) for post-metamorphic individuals by breeding season. Data are partitioned into adults (yellow bars), and yearlings (orange bars).

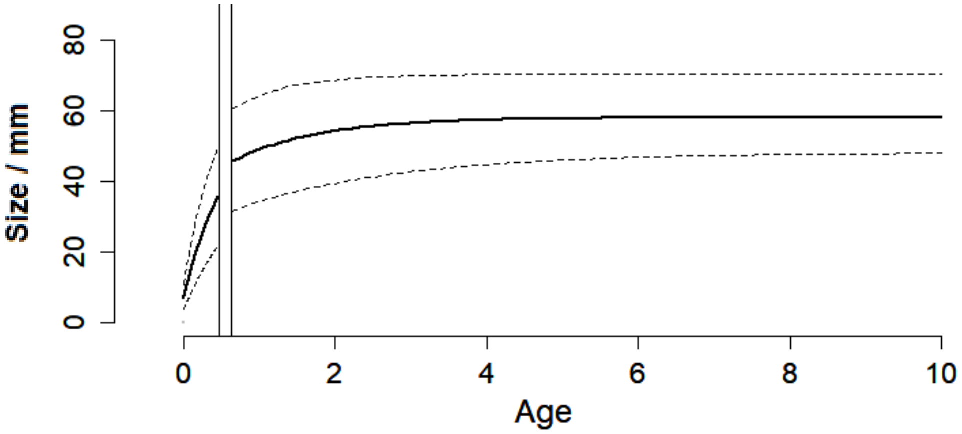

Figure 4. Predicted growth of reticulated flatwoods salamanders across both larval and adult stages. The two vertical lines represent the 95% credible intervals for minimum and maximum age at metamorphosis respectively, and the dashed lines represent 95% credible intervals. Length reflect snout-vent length (SVL) in mm.

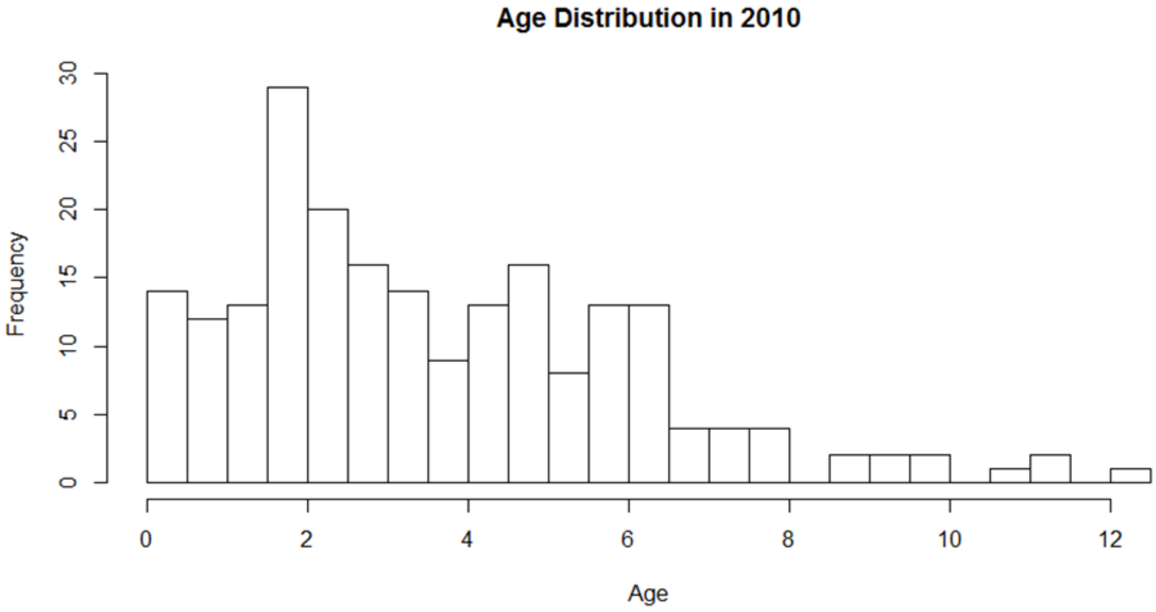

Figure 5. Predicted age distribution of adult flatwoods salamander at the start of the study. Average age of the population was between 4 and 5 years old; maximum longevity is 12-13 years.

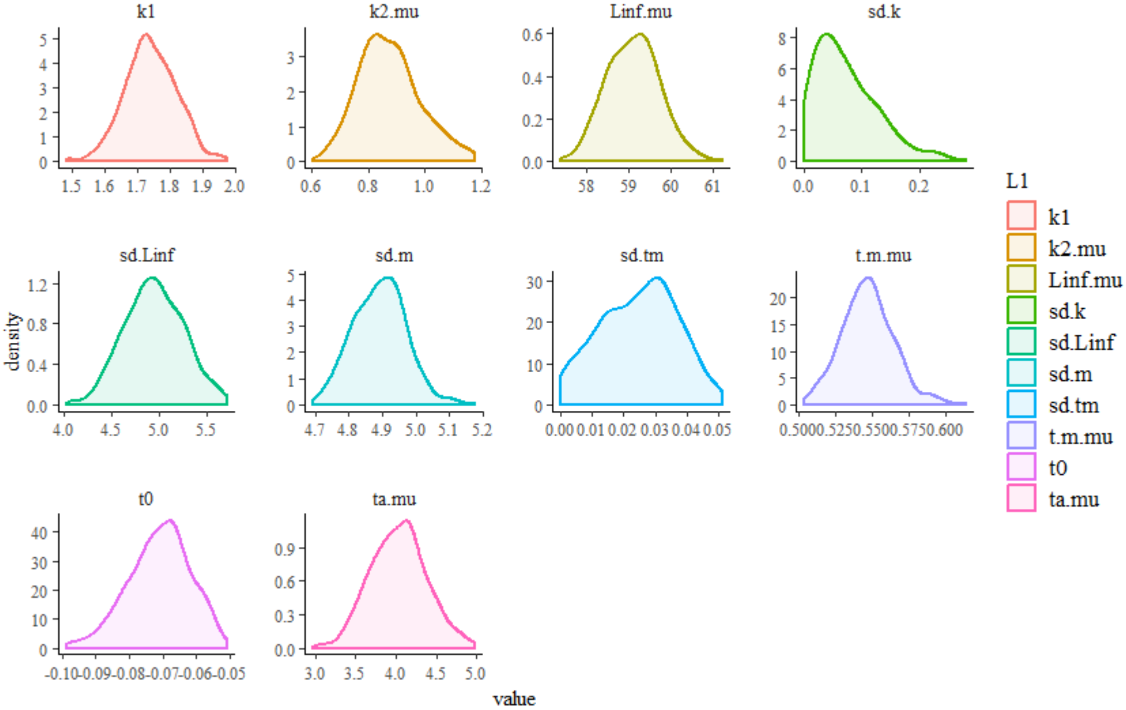

Figure 6. Posterior distributions for larval growth rate (k1), adult growth rate (k2), asymptotic size (Linf.mu), variability in growth rate and asymptote (sd.k and sd.Linf respectively), age at metamorphosis (t.m.mu), variability in age at metamorphosis (sd.tm), theoretical age at size zero (t0), average age of the adult population (ta.mu), and measurement error (sd.m).

CHAPTER 3

On the life-history consequences of size-dependence in amphibian survival

ABSTRACT

Survival is a key component of fitness and therefore fundamental to demographic models used to assess population viability. Such models can be used to evaluate alternative management strategies and predict extinction risk for species of conservation concern. However, most studies of wild populations suffer from right-censoring and left truncation, causing a considerable challenge to estimating survival. Survival rates are often correlated with life-history stage and body size, and thus change over the course of an individual’s lifetime. Longitudinal covariates, such as body size, are particularly difficult to include in survival analyses for rare or elusive species, because the size of the individual is unknown for sampling occasions when the individual was not observed. We integrated a von Bertalanffy growth model with a multi-state robust-design Cormack-Jolly-Seber model to test size-dependent survival in the Reticulated Flatwoods Salamander, *Ambystoma bishopi*. We adopt a Bayesian approach to model the uncertainty associated with the size of an individual when it was undetected, and use imputed values of body-size to discern patterns in survival rates. Typical of many organisms, *A. bishopi* exhibited a positive association between body size and survival; the smallest individuals experience twice the level of annual mortality risk compared with the largest individuals in the population. Survival estimates for *A. bishopi* provide insight into the life-history and demography of the species, and when combined with information on recruitment, will facilitate inferring persistence times of extant populations.

INTRODUCTION

Estimating survival of wild animals is challenging. Unlike clinical data for which time-to-event models were originally developed, 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 (Pike et al. 2008; Papadatou et al. 2012; Rose et al. 2018). Historically, in order to obtain survival estimates for elusive species, it was necessary to assume survival rates were constant (Pollock et al. 1990). Survival often varies amongst individuals, however, and quantifying this variation is necessary to understand and accurately predict population dynamics (Brooks et al. 2000; Rees and Ellner 2009). Inferring variability in survival from truncated, censored, and missing data respectively, has been a primary goal of survival analyses in ecology.

Individual histories with unknown times of death (right-censored) are readily accommodated by traditional Cormack-Jolly-Seber models, which treat the time of death as a latent variable to be estimated (Pledger et al., 2003, Pledger et al., 2010; Colchero and Clark 2012; Su and Wang 2012). Unknown birth dates (left-truncated) have posed more of a challenge and as a result have often been omitted from analyses (Bailey *et al.*, 2004, Matechou *et al.*, 2013). Yet for many species of conservation concern, small population sizes and short study durations relative to the generation times, make it undesirable to discard incomplete records from analyses.

In order to include animals whose birth went unobserved, models can divide populations into cohorts that are assumed to be the same age, and cohort is treated as a latent variable to be estimated (Letcher and Horton 2008, Kéry and Schaub 2011, Matechou et al. 2013). For well-established populations, it is also necessary to extend entry probabilities prior to the initial sampling occasion to include individuals that were born before the start of the study (Colchero and Clark 2012). By combining derived estimates of birth and death with a flexible mortality function, the analysis of left-truncated, right-censored data (LTRC) becomes possible (Colchero and Clark 2012, Matechou *et al.*, 2013).

Individual-specific traits such as size, age, and sex, can all influence survival probabilities in wild populations (Pollock et al. 1990; Lebreton et al. 1992; Ebenman and person 2012). Projection models that neglect variation in mortality risk amongst individuals can lead to erroneous conclusions regarding population status, potentially leading to flawed management decisions, thereby reducing the effectiveness of conservation measures (Ramula et al., 2009, Hegg et al., 2013). Discrete, time-invariant traits, such as sex, can readily be incorporated into survival analyses as covariates (Lebreton et al. 1992; Rose et al. 2018). Similarly, if individuals can be reliably aged at the initial capture occasion, it is trivial to include age as a sequential time-varying covariate (King et al. 2008; Caswell et al. 2018).

Modeling the relationship between survival and continuous, time-varying individual covariates (hereafter longitudinal covariates) poses more of a challenge, because the state of an individual is unknown for sampling occasions when the animal was not caught (Wulfsohn and Tsiatis 1997; Su and Wang 2012, Langrock and King 2013). This problem is exacerbated for studies with infrequent sampling events, or species with low capture probabilities (Su and Wang 2012; Rose et al. 2018). In situations where age cannot always be accurately estimated (Halliday et al. 1988), and longitudinal covariates are more tightly linked to individual fates (Kirkpatrick 1984; Hughes and Connell 1987; Sauer and Slade 1987; Easterling et al. 2000; Ebenman and Persson 2012; but see Caswell 1988; Moore et al. 2016), methods are desperately needed to jointly model longitudinal processes and time-to-event data.

Body size can directly influence an amphibian's vulnerability to desiccation, starvation, or competition (Laurie and Brown 1990, Janzen 1993, Sorci and Clobert 1999, Lind et al. 2008, Cabrera-Guzmán et al. 2013), and strongly determines exposure risk to gape-limited predators (Shine 1991, Forsman 1996, Kishida et al. 2009, Cabrera-Guzmán et al. 2013). For species with complex life-histories, body size can be the primary factor that determines successful transition between life-stages, with size at metamorphosis carrying long-term fitness effects on future survival and reproductive success (Wilbur and Collins 1973, Werner 1986, Semlitsch et al. 1988, Taylor and Scott 1997, Altwegg and Reyer 2003, De Block and Stoks 2005).

To include body size in survival analyses, the most common solution is to reduce it to a discrete covariate, such that inference concerning unobserved individuals can be drawn from observed individuals in the same size class (Caswell 2001, Lebreton and Pradel 2002, Letcher and Horton 2008). Alternatively, one can adopt a two-stage approach that first involves imputing values for the missing longitudinal processes, followed by a partial likelihood approach to estimate survival parameters of interest (Tsiatis et al. 1995; Su and Wang 2012). Treating these predicted values as observed data, however, ignores uncertainty in the missing values and will likely underestimate uncertainty or bias parameter estimates (Prentice 1982; Bonner et al. 2010; Su and Wang 2012).

Bayesian imputation has been suggested as a method to retain the uncertainty associated with imputed values, by using posterior distributions rather than point estimates as covariates of survival for those missing data (Bonner et al. 2010, Schofield and Barker 2011). The Bayesian approach offers the most practical method for modeling longitudinal covariates when detectability is low (Brooks et al. 2000; Bonner et al. 2010; Rose et al. 2018). Here we construct a modified parameterization of the Cormack-Jolly-Seber (CJS) model for flatwoods salamanders (*Ambystoma bishopi*) that includes continuous covariates and accounts for imperfect detection (Lebreton et al. 1992, Royle 2008). We find a strong positive association between survival and body size, seasonal differences in instantaneous survival rates, and annual variability in survival; all three of these characteristics can be incorporated into demographic models when assessing population viability.

MATERIALS AND METHODS

The classic state-space 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. Individuals can occupy one of three states: alive but unavailable for capture, alive and available for capture, and dead. Individuals that have not entered the population enter the population with probability gamma, and remain unavailable for capture with probability 1-gamma.

In this initial analysis, survival and detectability were assumed to be constant across years. Emigration is modelled as a Dirichlet process, conditional on the number of entrants in previous years (see Chapter 1 for details). Using a logit link function, we modelled survival as a linear function of body size at time of capture.

$$logit(\phi) = \mu + \beta X + \varepsilon$$

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

$$\bar{\phi} \sim Beta(1,1)$$

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

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

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 (White and Burnham 1999). Size estimates for unobserved individuals at each sampling occasion were interpolated using parameters estimated from the von Bertalanffy growth equation in Chapter 2. By adopting a hierarchical Bayesian approach, the uncertainty in imputed sizes is accounted for and reflected in survival estimates.

Individuals can occupy one of three states; 1 = not yet entered, 2 = alive and entered, 3 = dead. This results in the state transition matrix, $S(z_{i,t})$,

$$\begin{bmatrix} 1-\gamma & \gamma & 0 \\ 0 & \phi & 1-\phi \\ 0 & 0 & 1 \end{bmatrix}$$

where γ reflects year specific entry probabilities, and ϕ survival. Thus, at any given time, an individual's state (z) is modelled as

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

Observations were linked to the process model via a parameter that governs the probability of detection (p). For each sampling occasion, and individual is either seen (1), or not seen (2), yielding a 2x3 observation process matrix, $O(y_{i,t})$,

$$\begin{bmatrix} 0 & 1 \\ p & 1-p \\ 0 & 1 \end{bmatrix}$$

$$y_{i,t} | z_{i,t} \sim Bern(O(z_{i,t}))$$

$$p \sim Beta(1,1)$$

Given the sampling methodology, and owing to issues with identifiability, we did not include any covariate influence on recapture probabilities. Estimating survival from marked animals is complicated by emigration, making certain individuals unavailable for capture for part of the study duration. Failure to account for emigration (both temporary and permanent) outside of the study area will lead to negatively biased estimates of survival (Kendall et al. 1997; Gilroy et al. 2012). We fit a hierarchical, multi-state, robust-design Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) to estimate annual survival, temporary emigration, and detection probabilities. We adopted the robust-design formulation of CJS that treats the population as closed between sampling occasions within a season and open between years (Pollock 1982).

To corroborate our findings, we constructed a suite of simpler models to investigate additional factors affecting survival. By treating the last capture occasion as a proxy for apparent survival in a logistic regression framework, we were able to include season and year as covariates. Size, season, and year were included as fixed effects and all possible combinations of models were compared using Akaike information criterion (AIC; Akaike 1974). Using model selection procedures, we estimated the likelihood that each model is the most parsimonious, and used a ΔAIC cutoff of >4 to indicate an improvement in model fit (Burnham and Anderson 1998, Letcher and Horton 2008). AIC weights were calculated to discern the relative support for each model.

RESULTS

All model parameters adequately converged; all potential scale reductions factors (PSRF) for individual parameters were < 1.1. The multivariate PSRF for the full model was 1.06. Posterior p-values for survival, detection, and entry probabilities all approximated 0.5, indicating a good model fit.

Between Fall 2010 and Spring 2019, 1154 adult flatwoods salamanders at two breeding wetlands on Eglin Air Force Base were marked and released. The average snout-vent length (SVL) of the marked animals was 56 mm (sd = 7). In addition, 750 metamorphs were captured emerging from wetlands, but were excluded from the analysis to avoid bias introduced by unequal emigration rates. Following the initial capture occasion, 374 marked animals were recaptured on at least one occasion. Given two opportunities to encounter individuals each year (arrival and departure), and a drift fence design that completely encircles breeding wetlands, annual detection probabilities were surprisingly low (0.74, CI: 0.70-0.79). As we were unable to include a parameter governing the probability of skipping a breeding season, detectability may be artificially deflated by the confounding influence of temporary emigration.

Mean survival rate of adult salamanders regardless of season or size, was surprisingly low given the infrequency of recruitment in this species, and the well documented longevity of congeners (0.42, CI:0.30-0.71). Model estimates provided strong support for size-dependent and season-dependent survival in adult flatwoods salamanders. Estimated survival rates doubled as body size increased from 30 mm to 70 mm (Figure 1). In concordance with the results from the Bayesian analysis, models that included size consistently outperformed simpler models in the likelihood framework (Table 1). In addition, there was evidence for high variability in survival rates across years, with estimates highest in 2012 and lowest in 2017 (Figure 3). Survival estimates were consistently 10% lower during the non-breeding season compared with the breeding season across all sizes and years (Figure 3).

DISCUSSION

Regardless of the source, elevated mortality risk posed to smaller individuals is of paramount importance in shaping many facets of life-history. Salamanders are typically long-lived, with moderate clutch sizes, and make multiple breeding attempts throughout their lifespans (Petranka 1998). Such a bet-hedging strategy is predicted to arise when reproductive success in a given year is highly unpredictable (Cohen 1966). For ephemeral-pond breeding amphibians that regularly experience years of catastrophic reproductive failure, selection for increased longevity at the expense of current reproductive output appears favorable (Murphy 1968, Maiorana 1976). The role of environmental stochasticity in shaping life-history strategies and survival patterns in amphibians requires further investigation.

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. Ontogenetic shifts in vital rates can strongly influence a population’s vulnerability to exploitation and local extirpation (Letcher & Horton 2008, Van de Wolfshaar et al. 2008, Xu et al. 2010). In size-structured populations, survival rates are often a function of size and local environment (Cooch 2002, Letcher et al. 2002, Brown et al. 2004, Blums et al. 2005, Xu et al. 2010), and thus projection models that neglect patterns in mortality risk can lead to erroneous conclusions regarding population viability, with potentially disastrous consequences for management (Ramula et al., 2009, Hegg et al., 2013). Here we find evidence for size-dependent survival in flatwoods salamanders and distinct seasonal patterns in mortality.

The positive correlation between body size and survival is well established in nature (Roff 1992, Cooch 2002, Ebenman and Persson 2012). Many predators are gape-limited (Shine 1991, Forsman 1996), and thus larger body size reduces the number of potentially fatal encounters. Alternatively, energetic considerations could generate a similar pattern of size-dependent survival (Laurie and Brown 1990, Sorci and Clobert 1999). For amphibians particularly, regulation of temperature and water balance is more challenging at smaller sizes, with increasing surface area to body ratio (Duellman and Trueb 1994). Thus, smaller individuals are less able to survive prolonged periods of drought, temperature extremes, or food deprivation (Spotila 1972, Maiorana 1976, Ash et al. 2003, Knapp et al. 2003, Rothermel and Semlitsch 2006, Tilghman et al. 2012, Messerman et al. 2020). Our results indicate higher mortality in smaller individuals, but we cannot separate the relative contributions of predation and environment.

When conducting survival analyses of marked populations, it is important to acknowledge the interplay of true survival and site fidelity (Haas 1998, Letcher and Horton 2008, Gilroy et al. 2012). Unless assumptions of closure are met, estimates of true survival are confounded by losses other than mortality (Letcher and Horton 2008, Barbour et al. 2013). Particularly for pond-breeding amphibians, where juveniles are thought to represent the dispersal phase, higher rates of emigration in smaller individuals have the power to mask, or more likely exaggerate, size-survival relationships (Letcher and Horton 2008). Several previous salamander studies have documented transient behavior in more than 50% of individuals within a population (Schmidt et al. 2007, Lee et al. 2012, Unglaub et al. 2015, Lau et al. 2017), and thus, while 'apparent' survival may provide some information regarding individual fates, explicitly accounting for emigration is almost always preferable (Gilroy et al. 2012, Schaub and Royle 2014, Taylor et al. 2015, Bucciarelli et al. 2016). Unfortunately, for many species of conservation concern, the data required to account for biases in movement and site fidelity are often lacking (Ergon and Gardner 2014, Royle et al. 2014, Lau et al. 2017, Rose et al. 2018).

Survival studies must also consider biases introduced by variation in individual growth rates and recapture intervals. Undocumented changes in size preceding mortality are more likely for longer intervals between sampling occasions and for populations exhibiting stronger individual growth rate variation. If the period between sampling events is sufficiently long, size at time of death may not accurately reflect size at sampling, and estimates of size-dependent survival will be marred with uncertainty. Future work should attempt to quantify potential biases in survival estimates introduced by extended recapture intervals and variable growth rates. For studies such as this one, sampling periods are restricted to migration events, when animals are encountered at high enough abundances to justify survey effort. Clearly in these instances, the focal species' life-history precludes extensive modifications to sampling schemes, but in other cases such information can be used to guide the timing of surveys, such that data collected are more amenable for analysis.

Ectotherms are strongly influenced by environmental conditions and/or resource availability (Forsman 1991, Kunz and Ekman 2000). Flatwoods salamanders show evidence of seasonal patterns in growth, with individuals experiencing a cessation of growth in between breeding events, and a corresponding reduction in survival during this period. Salamanders are known to go into a negative energy budget at higher temperatures (Bobka et al. 1981, Homyack et al. 2010, 2011), and hence it is likely that the harsh Floridian summers drive the seasonal patterns in mortality we observe. Further, disparate environmental conditions are the most parsimonious explanation for annual variability in survival estimates. The sensitivity of amphibian vital rates to changes in the abiotic environment is a worrying portent, in light of future climate projections and land-use conversion (Blaustein et al. 2001, 2010, Corn 2005, Shoo et al. 2011, Foden et al. 2013, Yiming et al. 2013).

The tight link between environment and vital rates in amphibians has implications for conservation practices (Lawler et al. 2010, Shoo et al. 2011, Foden et al. 2013). Larval-headstarting is a common practice in amphibian conservation, as a means to subsidize natural recruitment, both in terms of the number and quality of recruits (Griffiths and Pavajeau 2008). Captive rearing affords the benefit of being much more readily able to manipulate temperature regimes and prey availability to influence larval growth. Developmental plasticity is well documented in larval amphibians; size at metamorphosis is positively correlated with prey abundance and temperature, and inversely related to larval density and duration of the larval period (Newman 1998, Morey and Reznick 2001, Alvarez and Nicieza 2002, Walsh et al. 2008, Indermaur et al. 2010, Richter-Boix et al. 2011). Hence, larval headstarting provides an experimental arena to investigate patterns of growth and survival, which will yield data to improve the efficacy of conservation efforts. For flatwoods salamanders, headstarting efforts tailored to achieving larger metamorphs than those produced naturally would be beneficial if a higher proportion of individuals survive their first summer and return to breed. The extent to which larval conditions carry over to impact adult populations however, remains uncertain (Werner 1986, Blanckenhorn 1998, Morey and Reznick 2001, Ficetola and Bernardi 2006, Richter-Boix et al. 2006, Cabrera-Guzmán et al. 2013). Clearly, elucidating the post-metamorphic effects of larval growth and body size should be a priority for future research efforts, in order to confirm the long-term impact of headstarting efforts (Searcy et al. 2014).

Conservation of pond-breeding amphibians has often neglected the terrestrial phase of the life-history. Species in the family Ambystomatidae are fossorial in the adult stage, and thus rarely observed and challenging to study post-metamorphosis. Terrestrial habitats cannot be overlooked, because adult populations serve as reservoirs during droughts or even between breeding seasons (Husting 1965; Whitford & Vinegar 1966, Dodd 1993, Semlitsch and Bodie 2003, Harper et al. 2008). Indeed, longevity in salamanders likely represents a storage effect (Warner and Chesson 1985), whereby adults must persist on the landscape in sufficient numbers to compensate for catastrophic reproductive failures in dry years (Palis et al. 2006, Taylor et al. 2006).

Given such life-history considerations, it is unsurprising that there is a growing body of literature demonstrating the sensitivity of amphibian populations to changes in adult survival rates (Biek et al. 2002; Vonesh & De la Cruz 2002, Harper et al. 2008). For purportedly long-lived species, reduced adult survival can act to reduce the number of breeding attempts in a lifetime, and may ultimately undermine population viability (Griffiths et al. 2010). Several facets of the terrestrial environment surrounding breeding wetlands have been shown to be the best predictor of amphibian diversity and/or abundance, including forest cover (Homan et al. 2004; Rubbo & Kiesecker 2005, Quesnelle et al. 2015), small mammal burrow density (Loredo et al. 1996), and distance to roads (Vos and Chardon 1998, Pillsbury and Miller 2008, Veysey et al. 2011). The importance of such factors suggests that wetland protection and restoration may be necessary but not sufficient to curb amphibian declines (Harper et al. 2008, Todd et al. 2014). Weighing the relative merits of aquatic vs. terrestrial management, and recommending a holistic approach to amphibian conservation, should be a primary goal.

Accurate estimates of survival are an invaluable component of demographic models, and have proven extremely useful when evaluating alternative management strategies and predicting the efficacy of conservation actions. Further, uncovering patterns of survival within populations can reveal why focal species are imperiled or potentially implicate agents of decline. Survival estimates for *A. bishopi* will give insight into the life-history and demography of the species; when combined with information on recruitment, they will provide managers with the information to infer persistence times of declining populations.

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LITERATURE CITED

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control, 19:716-723.

Altwegg, R., and Reyer, H.U. 2003. Patterns of natural selection on size at metamorphosis in water frogs. Evolution, 57:872–882.

Alvarez, D., and Nicieza, A.G. 2002. Effects of temperature and food quality on anuran larval growth and metamorphosis. Functional Ecology, 16:640–648.

Ash, A.N., Bruce, R.C., Castanet, J., and Francillon-Vieillot, H. 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., Kendall, W.L., Church, D.R., and Wilbur, H.M. 2004. Estimating survival and breeding probability for pond-breeding amphibians: A modified robust design. Ecology, 85:2456-2466.

Barbour, A.B., Ponciano, J.M., and Lorenzen, K. 2013. Apparent survival estimation from continuous mark–recapture/resighting data. Methods in Ecology and Evolution, 4:846-853.

Biek, R., Funk, W.C., Maxell, B.A., and Mills, L.S. 2002. What is missing in amphibian decline research: insights from ecological sensitivity analysis. Conservation Biology, 16:728–734.

Blanckenhorn, W.U. 1998. Adaptive phenotypic plasticity in growth, development, and body size in the yellow dung fly. Evolution, 52:1394–1407.

Blaustein, A.R., Belden, L.K., Olson, D.H., Green, D.M., Root, T.L., and Kiesecker, J.M. 2001. Amphibian breeding and climate change. Conservation Biology, 15:1804-1809.

Blaustein, A.R., Walls, S.C., Bancroft, B.A., Lawler, J.J., Searle, C.L., and Gervasi, S.S. 2010. Direct and indirect effects of climate change on amphibian populations. Diversity, 2:281-313.

Blums, P., Nichols, J.D., Hines, J.E., Lindberg, M.S., and Mednis, A. 2005. Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. Oecologia, 143:365–376.

Bobka, M.S., Jaeger, R.G., and McNaught, D.C. 1981. Temperature dependent assimilation efficiencies of two species of terrestrial salamanders. Copeia, 417-421.

Bonner, S.J., Morgan, B.J.T., and King, R. 2010. Continuous covariates in mark-recapture-recovery analysis: a comparison of methods. Biometrics, 66:1256–1265.

Brooks, S.P., Catchpole, E.A., and Morgan, B.J. 2000. Bayesian animal survival estimation. Statistical Science, 15:357-376.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., and West, G.B. 2004. Toward a metabolic theory of ecology. Ecology, 85:1771–1789.

Bucciarelli, G.M., Green, D.B., Shaffer, H.B., and Kats, L.B. 2016. Individual fluctuations in toxin levels affect breeding site fidelity in a chemically defended amphibian. Proceedings of the Royal Society B: Biological Sciences, 283.

Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer Verlag, New York.

Cabrera-Guzmán, E., Crossland, M.R., Brown, G.P., and Shine, R. 2013. Larger body size at metamorphosis enhances survival, growth and performance of young cane toads (*Rhinella marina*). PLoS One, 8:e70121.

Caswell, H. 1988. Approaching size and age in matrix population models. pp. 85-105 In B. Ebenman (eds), Size-structured populations. Springer, Berlin, Heidelberg.

Caswell, H. 2001. Matrix population models. construction, analysis and interpretation. Sinauer Associates, Sunderland

Caswell, H., de Vries, C., Hartemink, N., Roth, G., and van Daalen, S.F. 2018. Age× stage-classified demographic analysis: a comprehensive approach. Ecological Monographs, 88:560-584.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. Journal of Theoretical Biology, 12:119-129.

Colchero, F., and Clark, J.S. 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 Stoks, R. 2005. Fitness effects from egg to reproduction: bridging the life history transition. Ecology, 86:185–197.

Dodd Jr, C.K. 1993. Cost of living in an unpredictable environment: the ecology of striped newts *Notophthalmus perstriatus* during a prolonged drought. Copeia, 605-614.

Duellman, W.E., and Trueb, L. 1994. Biology of amphibians. JHU press.

Easterling, M.R., Ellner, S.P., and Dixon, P.M. 2000. Size-specific sensitivity: applying a new structured population model. Ecology, 81:694-708.

Ebenman, B., and Persson, L. 2012. Size-structured populations: ecology and evolution. Springer Science & Business Media.

Ergon, T., and Gardner, B. 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.

Ficetola, G.F., and De Bernardi, F. 2006. Trade-off between larval development rate and post-metamorphic traits in the frog *Rana latastei*. Evolutianry Ecology, 20:143–158.

Foden, W.B., Butchart, S.H., Stuart, S.N., Vié, J.C., Akçakaya, H.R., Angulo, A., DeVantier, L.M., Gutsche, A., Turak, E., Cao, L., and Donner, S.D. 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.

Gilroy, J.J., Virzi, T., Boulton, R.L., and Lockwood, J.L. 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 Pavajeau, L. 2008. Captive breeding, reintroduction, and the conservation of amphibians. Conservation Biology, 22:852-861.

Griffiths, R.A., Sewell, D., and McCrea, R.S. 2010. Dynamics of a declining amphibian metapopulation: survival, dispersal and the impact of climate. Biological Conservation, 143:485-491.

Halliday, T., and Verrell, P. 1988. Body size and age in amphibians and reptiles. Journal of Herpetology, 22:253–265.

Harper, E.B., Rittenhouse, T.A., and Semlitsch, R.D. 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., MacKenzie D.I., and Jamieson I.G. 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.

Homan, R.N., Windmiller, B.S., and Reed, J.M. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. Ecological Applications, 14:1547–1553.

Homyack, J.A., Haas, C.A., and Hopkins, W.A. 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., Haas, C.A., and Hopkins, W.A. 2011. Energetics of surface-active terrestrial salamanders in experimentally harvested forest. Journal of Wildlife Management, 75:1267-1278.

Hughes, T.P., and Connell, J.H. 1987. Dynamics based on size or age? A reef-coral analysis. American Naturalist, 129:818–829.

Husting, E.L. 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. Copeia, 1965:352–362.

Indermaur, L., Schmidt, B.R., Tockner, K., and Schaub, M. 2010. Spatial variation in abiotic and biotic factors in a floodplain determine anuran body size and growth rate at metamorphosis. Oecologia, 163:637–649.

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.

Kendall, W.L., Nichols, J.D., and Hines, J.E. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology, 78:563–578.

Kéry, M., and Schaub, M. 2011. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press.

Kirkpatrick, M. 1984. Demographic models based on size, not age, for organisms with indeterminate growth. Ecology, 65:1874-1884.

Kishida, O., Trussell, G.C., Nishimura, K., and Ohgushi, T. 2009. Inducible defenses in prey intensify predator cannibalism. Ecology, 90:3150–3158.

Knapp, S.M., Haas, C.A., Harpole, D.N., and Kirkpatrick, R.L. 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. Conservation Biology, 17:752-762.

Kunz, C., and Ekman, J. 2000. Genetic and environmental components of growth in nestling blue tits (*Parus caeruleus*). Journal of Evolutionary Biology, 13:199–212.

Langrock, R., and King, R. 2013. Maximum likelihood estimation of mark–recapture–recovery models in the presence of continuous covariates. The Annals of Applied Statistics, 7:1709-1732.

Lau, A., Karraker, N.E., and Dudgeon, D. 2017. Does forest extent affect salamander survival? Evidence from a long-term demographic study of a tropical newt. Ecology and Evolution, 7:10963-10973.

Laurie, W.A., and Brown, D. 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., Shafer, S.L., Bancroft, B.A., and Blaustein, A.R. 2010. Projected climate impacts for the amphibians of the Western Hemisphere. Conservation Biology, 24:38-50.

Lebreton, J.D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modelling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs, 62:67–118.

Lebreton, J.D., and Pradel, R. 2002. Multistate recapture models: modelling incomplete individual histories. Journal of Applied Statistics, 29:353–369.

Lee, D.E., Bettaso, J.B., Bond, M.L., Bradley, B.R., Tietz, J.R., and Warzybok, P.M. 2012. Growth, age at maturity, and age-specific survival of the Arboreal salamander (*Aneides lugubris*) on Southeast Farallon Island, California. Journal of Herpetology, 46:64-71.

Letcher, B.H., Gries, G., and Juanes, F. 2002. Survival of stream-dwelling Atlantic salmon: effects of life history variation, season and age. Transactions of American Fisheries Society, 131:838–854.

Letcher, B.H., and Horton, G.E. 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., Persbo, F., and Johansson, F. 2008. Pool desiccation and developmental thresholds in the common frog, *Rana temporaria*. Proceedings of the Royal Society B: Biological Science, 275:1073–1080.

Loredo, I., Van Vuren, D. and Morrison, M.L. 1996. Habitat use and migration behavior of the California tiger salamander. Journal of Herpetology, 30:282–285.

Maiorana, V.C. 1976. Size and environmental predictability for salamanders. Evolution, 599-613.

Matechou, E., Pledger, S., Efford, M., Morgan, B.J.T., Thomson, D.L., and Gimenez, O. 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.

Messerman, A.F., Semlitsch, R.D., and Leal, M. 2020. Estimating survival for elusive juvenile pond-breeding salamanders. The Journal of Wildlife Management, 84:562–575.

Moore, J.L., Lipcius, R.N., Puckett, B., and Schreiber, S.J. 2016. The demographic consequences of growing older and bigger in oyster populations. Ecological Applications, 26:2206-2217.

Morey, S., and Reznick, D. 2001. Effects of larval density on postmetamorphic spadefoot toads (*Spea hammondii*). Ecology, 82:510–522.

Murphy, G.I. 1968. Pattern in life history and the environment. The American Naturalist, 102:391-403.

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.

Palis, J.G., Aresco, M.J., and Kilpatrick, S. 2006. Breeding biology of a Florida population of *Ambystoma cingulatum* (Flatwoods salamander) during a drought. Southeastern Naturalist, 5:1-8.

Papadatou, E. 2012. Comparing survival among species with imperfect detection using multilevel analysis of mark–recapture data: a case study on bats. Ecography, 35:153–161.

Pike, D.A., Pizzatto, L., Pike, B.A., and Shine, R. 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. Ecology, 89:607–611.

Pillsbury, F.C., and Miller, J.R. 2008. Habitat and landscape characteristics underlying anuran community structure along an urban–rural gradient. Ecological Applications, 18:1107–1118.

Pledger, S., Pollock, K.H., and Norris, J.L. 2003. Open capture-recapture models with heterogeneity: I. Cormack-Jolly-Seber model. Biometrics, 59:786-794.

Pledger, S., Pollock, K.H., Norris, J.L. 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., Nichols, J.D., Brownie, C., and Hines, J.E. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs, 107:3–97.

Prentice, R. 1982. Covariate measurement errors and parameter estimates in a failure time regression model. Biometrika, 69:331-342.

Quesnelle, P.E., Lindsay, K.E., and Fahrig, L. 2015. Relative effects of landscape-scale wetland amount and landscape matrix quality on wetland vertebrates: a meta-analysis. Ecological Applications, 25:812-825.

Ramula, S., Rees, M., and Buckley, Y.M. 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 Ellner, S.P. 2009. Integral projection models for populations in temporally varying environments. Ecological Monographs, 79:575-594.

Richter-Boix, A., Llorente, G.A., and Montori, A. 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., Tejedo, M., and Rezende, E.L. 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.

Rose, J.P., Wylie, G.D., Casazza, M.L., and Halstead, B.J. 2018. Integrating growth and capture–mark–recapture models reveals size-dependent survival in an elusive species. Ecosphere, 9:e02384.

Rothermel, B.B., and Semlitsch, R.D. 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.

Royle, J.A., Chandler, R.B., Sollman, R., and Gardner, B. 2014. Spatial capture-recapture. Academic Press, Waltham, Massachusetts, USA.

Rubbo, M.J., and Kiesecker, J.M. 2005. Amphibian breeding distribution in an urbanized landscape. Conservation Biology, 19:504–511.

Sauer, J.R., and Slade, N.A. 1987. Uinta ground squirrel demography: Is body mass a better categorical variable than age? Ecology, 68:642–650.

Schaub, M., and Royle, J.A. 2014. Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. Methods in Ecology and Evolution, 5:1316-1326.

Schmidt, B.R., Schaub, M., and Steinfartz, S. 2007. Apparent survival of the salamander *Salamandra salamandra* is low because of high migratory activity. Frontiers in Zoology, 4:19.

Schofield, M.R., and Barker, R.J. 2011. Full open population capture–recapture models with individual covariates. Journal of Agricultural, Biological, and Environmental Statistics, 16:253–268.

Searcy, C.A., Gray, L.N., Trenham, P.C., and Shaffer, H.B. 2014. Delayed life history effects, multilevel selection, and evolutionary trade-offs in the California tiger salamander. Ecology, 95:68-77.

Seber, G.A.F. 1965. A note on the multiple-recapture census. Biometrika, 52:249–259.

Semlitsch, R.D., Scott, D.E., and Pechmann, J.H. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. Ecology, 69:184-192.

Semlitsch, R.D., and Bodie, J.R. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology, 17:1219-1228.

Shine, R. 1991. Why do larger snakes eat larger prey items? Functional Ecology, 5:493-502.

Shoo, L.P., Olson, D.H., McMenamin, S.K., Murray, K.A., Van Sluys, M., Donnelly, M.A., Stratford, D., Terhivuo, J., Merino-Viteri, A., Herbert, S.M., and Bishop, P.J. 2011. Engineering a future for amphibians under climate change. Journal of Applied Ecology, 48:487-492.

Sorci, G., and Clobert, J. 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.

Su, Y.R., and Wang, J.L. 2012. Modeling left-truncated and right-censored survival data with longitudinal covariates. Annals of Statistics, 40:1465.

Taylor, B.E., and Scott, D.E. 1997. Effects of larval density dependence on population dynamics of *Ambystoma opacum*. Herpetologica, 53:132-145.

Taylor, B.E., Scott, D.E., and Gibbons, J.W. 2006. Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. Conservation Biology, 20:792-801.

Taylor, C.M., Lank, D.B., and Sandercock, B.K. 2015. Using local dispersal data to reduce bias in annual apparent survival and mate fidelity. The Condor: Ornithological Applications, 117:598-608.

Tilghman, J.M., Ramee, S.W., and Marsh, D.M. 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. Biological Conservation, 152:1-9.

Todd, B.D., Blomquist, S.M., Harper, E.B., and Osbourn, M.S. 2014. Effects of timber harvesting on terrestrial survival of pond-breeding amphibians. Forest Ecology and Management, 313:123–131.

Tsiatis, A.A., and Davidian, M. 2004. Joint modeling of longitudinal and time-to-event data: An overview. Statistica Sinica, 14:809–834.

Tsiatis, A.A., DeGruttola, V., and Wulfsohn, M. 1995. Modeling the relationship of survival to longitudinal data measured with error: Applications to survival and CD4 counts in patients with AIDS. Journal of American Statistical Association. 90:23–37.

Unglaub, B., Steinfartz, S., Drechsler, A., and Schmidt, B.R. 2015. Linking habitat suitability to demography in a pond-breeding amphibian. Frontiers in Zoology, 12:9.

Van de Wolfshaar, K.E., De Roos, A.M., and Persson, L. 2008. Population feedback after successful invasion leads to ecological suicide in seasonal environments. Ecology, 89:259–268.

Veysey, J.S., Mattfeldt, S.D., and Babbitt, K.J. 2011. Comparative influence of isolation, landscape, and wetland characteristics on egg-mass abundance of two pool-breeding amphibian species. Landscape Ecology, 26:661–672.

Vonesh, J.R., and De la Cruz, O. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia, 133:325–333.

Vos, C.C., and Chardon, J.P. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. Journal of Applied Ecology, 35:44–56.

Walsh, P.T., Downie, J.R., and Monaghan, P. 2008. Temperature-mediated morphology changes during metamorphic climax in the African clawed frog, *Xenopus laevis*. Journal of Thermal Biology, 33:244–249.

Warner, R.R., and Chesson, P.L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. The American Naturalist, 125:769-787.

Werner, E.E. 1986. Amphibian metamorphosis: Growth rate, predation risk, and the optimal size at transformation. American Naturalist, 128:319–341.

Whitford, W.G., and Vinegar, A. 1966. Homing, survivorship, and overwintering of larvae in spotted salamanders, *Ambystoma maculatum*. Copeia, 517–519.

Wilbur, H.M., and Collins, J.P. 1973. Ecological aspects of amphibian metamorphosis. Science, 182:1305–1314.

Wulfsohn, M.S., and Tsiatis, A.A. 1997. A joint model for survival and longitudinal data measured with error. Biometrics, 53:330–339.

Xu, C.L., Letcher, B.H., and Nislow, K.H. 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.

Yiming, L.I., Cohen, J.M., and Rohr, J.R. 2013. Review and synthesis of the effects of climate change on amphibians. Integrative Zoology, 8:145-161.

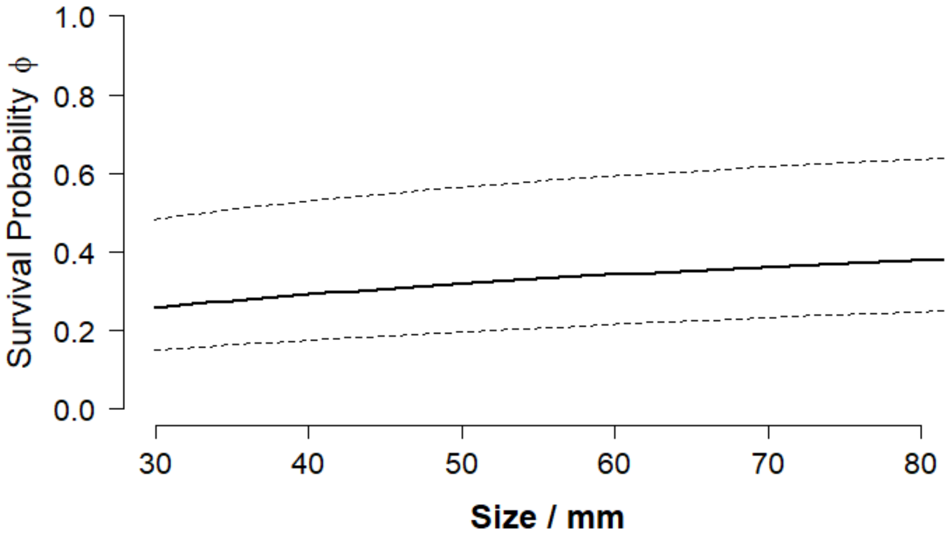

Figure 1. Size-dependent survival estimates for adult reticulated flatwoods salamanders. Estimates were obtained from a Cormack-Jolly-Seber parameterization modified to include body size as a continuous covariate. Size shown is snout-vent length (SVL) in mm. Solid lines reflect posterior mean, and dashed lines indicate 75% credible intervals.

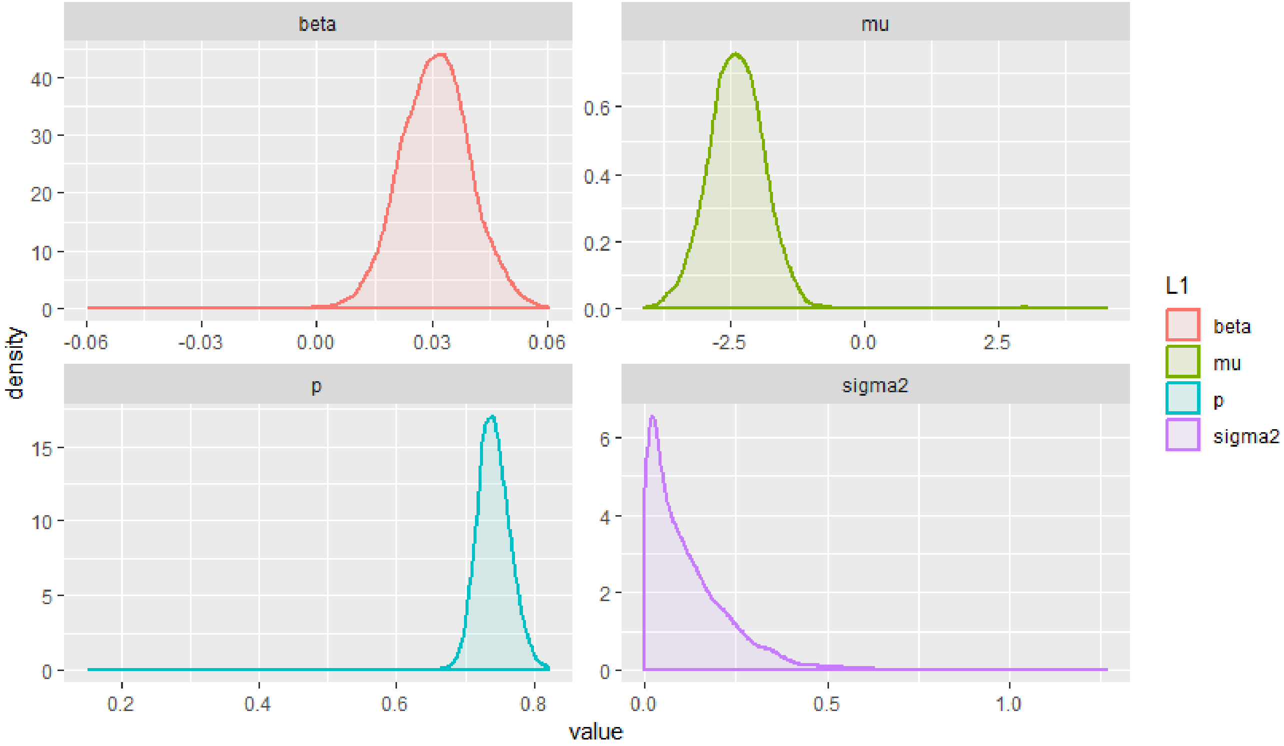

Figure 2. Posterior distributions of detection probability (p), mean survival on the logit scale (mu), slope of relationship between size and survival (beta), and residual standard deviation (sigma2) from the Cormack-Jolly-Seber model.

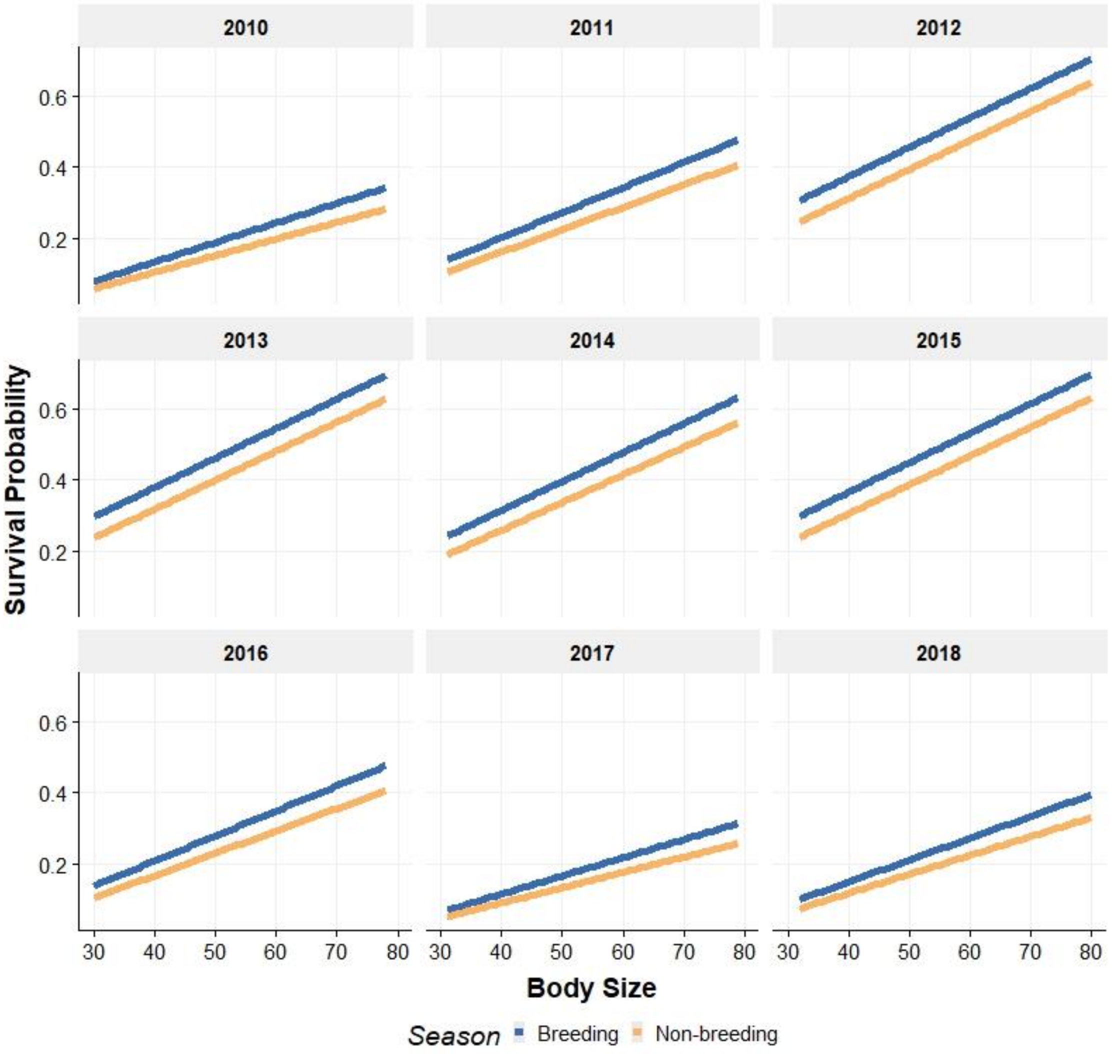

Figure 3. Size-dependent survival estimates for flatwoods salamanders by year and season (e.g. the panel for 2010 represents the 2010-2011 breeding season, and the subsequent non-breeding season). The breeding season typically encompasses the months of October through March, but residency times vary annually with environmental conditions. Body size reflects snout-vent length (SVL) in mm.

Table 1. Comparison of models of reticulated flatwoods salamander survival, with and without survival covariates. S(*) indicates models that treat survival as fixed, S(Size, Season, Year) indicates a model that treats survival as a function of body size, season (breeding vs. non-breeding), and year. w_i refers to AIC weights.

Model	AIC	ΔAIC	w_i
S(Size, Season, Year)	2184.7	0.0	0.84
S(Size, Year)	2188.0	3.3	0.16
S(Season, Year)	2202.3	17.6	0.00
S(Year)	2205.0	20.3	0.00
S(Size, Season)	2278.6	93.9	0.00
S(Size)	2285.9	101.2	0.00
S(Season)	2306.5	121.9	0.00
S(*)	2312.3	127.6	0.00

CHAPTER 4

Population viability of an endangered amphibian under future management scenarios

ABSTRACT

Population viability analyses (PVAs) represent a key component of many recovery plans for threatened and endangered species. Demography links the processes that affect individuals to population-level patterns, and hence projections constructed from demographic data are the most common tools for PVAs. Integral projection models (IPMs) allow vital rates to be governed by continuous traits, such as body size or weight. We evaluated demographic influences on population growth of Reticulated Flatwoods Salamanders, *Ambystoma bishopi*, and demonstrated potential avenues for predicting the efficacy of future management actions for this U.S. federally endangered species. Flatwoods salamanders breed in ephemeral wetlands in the Southeastern U.S. The ephemeral nature of breeding sites can result in complete recruitment failure in drought years when wetlands fail to fill, or dry before metamorphosis occurs. As a result, this species exhibits marked temporal variability in vital rates that must be accounted for in projection models. We constructed a stochastic IPM from eight years of mark-recapture data, and parameterized models in a Bayesian framework. Flatwoods salamanders exhibited relatively low survival rates compared to congeners and a high probability of recruitment failure, which resulted in a low predicted probability of population persistence. Sensitivity analyses revealed large-bodied, mature females exert the greatest influence on population growth, and thus managers should prioritize conservation efforts that target this life stage. Additional management should seek to dampen temporal

variability in larval survival, something that could be achieved through captive rearing efforts and restoration of pond hydroperiods.

INTRODUCTION

Demography links the processes that affect individuals to population-level patterns. Demographic analysis has its origins in studies of human populations, that used age-structured models to investigate rates of survival, fertility, and population growth (e.g., Malthus 1872, Lotka 1939, Coale 1972). Ecologists were quick to co-opt these methods to model the population dynamics of animal populations (Deevey 1947, Leslie and Park 1949, Cole 1954). Such analytical tools have contributed to both theoretical and applied fields; demographic models underpin assessments of wildlife populations to address practical problems in conservation (Akçakaya and Sjögren-Gulve 2000), and also serve as the foundation for life-history theory (Stearns 1992).

Population viability analysis (PVA) is a modelling framework that uses demographic data from individual species to evaluate extinction risk, causative agents of decline, and management strategies to promote future recovery (Akçakaya and Sjögren-Gulve 2000, Beissinger and McCullough 2002). PVAs are preferred over alternative methods to guide conservation decisions (e.g., Habitat Suitability Indices, HSIs; Gap analyses; IUCN criteria) owing to their ability to account for uncertainty in population parameters, the flexibility that allows the amalgamation of multiple, disparate data types, and the ease with which outputs directly translate to management recommendations (Akçakaya and Sjögren-Gulve 2000, Himes-Boor 2014, Oppel et al. 2014). When considering conservation strategies, there is a trade-off between expediency and careful evaluation of the myriad options available to managers; PVAs balance these two opposing forces by providing a mechanism to compare options in a way that quickly identifies the most appropriate path forward and facilitates rapid implementation (Platt 1964, Chamberlain 1965, Beissinger and McCullough 2002, Brook et al. 2002, van Poorten et al. 2019).

PVAs have been criticized for the relatively large amount of data they require, often precluding analysis for rare or understudied species that are typically the focus of conservation (Beissinger and McCullough 2002, Lotts et al. 2004, Weiss-Lehman et al. 2017, García-Díaz et al. 2019). Even with data-poor species, the process of developing a PVA can serve to highlight gaps in our knowledge, and can point the way forward for future investigations (Heppell et al. 2000, Coulson et al. 2001, Beissinger and McCullough 2002, Brook et al. 2002, Oppel et al. 2014). Hence, PVAs remain a fundamental component of many recovery plans (Brook 2000, Coulson *et al.* 2001, Himes Boor 2013).

Opponents also cite the unreliability of PVAs, and the tendency for researchers to downplay the uncertainty of model predictions (Taylor 1995, Ludwig 1996, 1999, Ellner et al. 2002, Patterson and Murray 2008, Bell et al. 2013, Morrison et al. 2013). The historical ‘abuse’ of PVAs stems from a lack of understanding of model limitations, and few instances of model validation (Coulson et al. 2001, Brook et al. 2002, Bell et al. 2013, Jäkäläniemi et al. 2013). This statistical illiteracy is not a problem unique to PVAs however; the unfettered implementation of statistical methods in ecology is rife and of salient concern. Such pitfalls can be avoided by honestly reporting associated uncertainties, and acknowledging that PVAs should only be used to make qualitative (not quantitative) predictions (Coulson et al. 2001, Brook et al. 2002, Ellner et al. 2002, McCarthy et al. 2003, Oppel et al. 2014, Weiss-Lehman et al. 2017). Further, PVAs should be implemented in an adaptive framework, whereby models are tested against real data and refined accordingly (Akçakaya and Sjögren-Gulve 2000, Bakker and Doak 2009, Green and Bailey 2015). Conservation must be synergistic and cyclical, such that management is guided by modelling outcomes, and models are guided by management outcomes.

Despite the global concern over amphibian declines (Alford & Richards 1999; Houlahan et al. 2000; Collins & Storfer 2003), quantitative models have only received limited application to the problem (Biek et al. 2002, Schmidt et al. 2005, but see Halley et al. 1996). Further, many studies attempting to diagnose amphibian declines have limited their focus to a single vital rate (Biek et al. 2002; Forbes & Calow 2002; Vonesh & De la Cruz 2002, Schmidt et al. 2005), or to individual-level effects (Kiesecker et al. 2001; Boone & Bridges 2003, Schmidt et al. 2005), despite population growth being the quantity of interest (Crouse et al. 1987; Fujiwara & Caswell 2001; Forbes & Calow 2002, Schmidt et al. 2005).

Despite amphibian conservation efforts largely focusing on investigations of egg and larval stages, due to the difficulty in studying terrestrial stages, there is a strong appreciation for the influence of adult survival on population growth (Taylor & Scott 1997; Biek et al. 2002; Hels & Nachman 2002; Vonesh & De la Cruz 2002, Schmidt et al. 2005). The stochastic nature of recruitment in many ephemeral pond breeders is also thought to be a rate-limiting step (Wilbur & Collins 1973; Wilbur 1980; Pechmann & Wilbur 1994; Alford & Richards 1999; Kiesecker et al. 2001; Schmidt et al. 2002, Boone & Bridges 2003; Semlitsch 2003, Schmidt et al. 2005). Demographic models can be used to assess whether adult survival or recruitment exert a greater influence on population viability.

Here we construct an integral projection model (IPM) for flatwoods salamanders, and estimate extinction risk under different recruitment scenarios that attempt to mimic future climate change and proposed management strategies. We performed a sensitivity analysis of the demographic model to identify components of the life history that exert the greatest influence on population growth. Ecological sensitivity analysis can be used to diagnose population declines, prioritize future research, and ultimately guide management efforts for imperiled species. Previous research has shown that post-metamorphic vital rates and variability in vital rates drive population dynamics of many pond-breeding amphibians, particularly long-lived species (Biek et al. 2002, Harper et al. 2008).

MATERIALS AND METHODS

Matrix projection models (MPMs) are the most popular form of structured population models owing to their simple structure and the useful metrics they provide to evaluate both population growth rate and the sensitivities of growth to changes in life-history components (Caswell 2001). Initially age-based (Leslie 1945), the complex life-histories and indeterminant growth seen in many species, particularly plants, led to the development of matrix models classified by stage (Lefkovitch 1965, Salguero-Gomez et al. 2015). Stage-structured models are more flexible than age-structured models, as stage can refer to body size, instar, breeding status, etc. Further, stage-structured models have been extended to include environmental stochasticity, seasonality, and density-dependence (Nisbet and Gurney 1982, Tuljapurkar 1990, Easterling et al. 2000, Caswell

2001, Ellner et al. 2016, Caswell et al. 2018). Despite this flexibility, and the greater biological realism that can be achieved with stage-structured populations, the majority of animal studies still rely on age-based models (Salguero-Gomez et al. 2016, Caswell et al. 2018).

Regardless of structure (age vs. stage), MPMs are forced to make simplifications that are seldom justified (Caswell 2001). For computational tractability, continuous populations have to be partitioned into discrete classes, whereby all individuals within a class are treated as identical. Increasing the number of discrete classes quickly becomes intractable, as each class warrants unique parameters to specify fecundity, survival, and state-transition rates (Easterling et al., 2000, Ramula and Lehtilä 2005). These concessions can potentially bias derived estimates of population growth, and weaken the conclusions that can be drawn from projection simulations (Enright et al., 1995, Easterling et al. 2000, Caswell 2001). Owing to the same simplifications, traditional matrix models often misrepresent transient dynamics, and are therefore inadequate for addressing questions related to the impact of continuous traits on ecological and evolutionary processes (Rees et al., 2014).

Integral projection models (IPMs) avoid the artificial partitioning of continuous traits necessary in traditional MPMs (Easterling et al. 2000). IPMs assume that individuals within a population extend over a continuous spectrum for particular quantitative traits, most often body size, whilst minimizing the number of new parameters that must be estimated (Merow et al., 2014). IPMs describe how a continuously structured population changes in discrete time with “kernels”, analogous to a non-zero projection matrix, representing every possible demographic transition for a given time interval (Easterling et al., 2000). Thus, underlying this population model is an individual-based model, following Markovian growth trajectories and with mortality and fecundity dependent on an individual's size. Each vital rate is modelled as a function of the initial body size, such that

$$k(x,y) = g(x,y)s(x) + f(x,y)$$

where k(x,y) is the complete IPM kernel, g(x,y) represents the probability distribution that an individual of size x grow to size y, s(x) is a size-dependent survival function, and f(x,y) combines fecundity, the probability that an adult female breeds in a given year, the probability that offspring survive to maturity, and the size distribution of new recruits. Size-specific fecundity estimates were obtained from the literature (Goin 1950, Anderson and Williamson 1976); estimates of the probability of reproducing and recruit size were derived from observed data (see Chapter 2, Figure 2); the size density of new recruits was parameterized as a normal distribution with mean constrained by the minimum and maximum observed sizes at metamorphosis and standard deviation 3 (SD derived from natural cohorts, see chapter 1). Complete recruitment failures are modelled as independent Bernoulli trials, with probability of successful recruitment for a given year derived from the observed probability over the course of the study (R = 0.3). Extinction probabilities were calculated for alternative values of R to investigate the sensitivity of population growth to recruitment failure.

Initially, IPMs were fully deterministic and density-independent; since their implementation however, IPMs have been extended in similar fashion to MPMs, and can now incorporate stochasticity, seasonality, and density-dependence (Childs et al., 2004, Rees and Ellner 2009, Vendenes et al. 2011, Coulson, 2012). Average population growth rate is reduced by stochastic fluctuations, and thus incorporating stochasticity into demographic models is important for reliable inference (Lewontin and Cohen 1969, Ellner and Rees 2007). Here we construct a stochastic IPM for flatwoods salamanders that accounts for uncertainty in vital rate parameters. Vital rates estimates are randomly drawn from the posterior distributions of constructed models (Chapters 2 and 3) to generate unique kernels each time-step in the projection (Ellner and Rees 2007, Rees and Ellner 2009, Vendenes et al. 2011, Ureta et al. 2012). For each parameterization of recruitment failure, the IPM was iterated 5000 times, with the first 1000 iterations discarded as burn-in. Extinction probabilities, the proportion of simulations that decline to zero, were calculated by simulating 1000 populations and projecting it 50 years into the future. The stochastic growth rate (λ_S) for each simulation was calculated as the geometric mean of the annual growth rates (Ellner and Rees 2007, Ureta et al. 2012), and we calculated the elasticity of λ_S to changes in both survival-growth and fecundity kernels (Easterling et al., 2000). Lastly, elasticity evenness, a metric that appears to correlate highly with extinction risk, was estimated following Van Allen et al. (2012). All analyses were conducted in R (R Core Team, 2018).

RESULTS

Under a business-as-usual scenario, these flatwoods salamander populations are likely to go extinct. The median long-term population growth rate (λ) derived from 1000 simulations was marginally less than 1, however sporadic recruitment driven by environmental stochasticity resulted in a high degree of uncertainty in long term population growth (Figure 1). Further, given the low probability of recruitment, λ exhibited a strong positive skew, as for most years recruitment is zero, and thus the only contribution to population growth is via mortality (Figure 1). Over half of all simulations for the baseline model decreased to zero within 50 years (Figure 2). Further, many of the simulations that persisted over the 50-year projection experienced years of perilously low population sizes following several years of zero recruitment.

Extinction probabilities are drastically reduced when recruitment occurs on average every other year, compared with every three years (Figure 2). In concordance, the median long-term growth rate for populations in this scenario was greater than 1, but the distribution of estimates still exhibited positive skew (Figure 1). Conversely, extinction after 50 years becomes certain when there is only a one in four chance of successful recruitment each year (results not shown).

Elasticity analysis highlights the joint contributions of recruitment and survival to population growth (Figure 3, 4). In years without recruitment, survival of large, fully-grown individuals exerted the greatest influence on long-term viability, with the contribution of individuals decreasing with body size (Figure 3). In years with successful recruitment, the fecundity component of the kernel strongly influenced population growth. Specifically, individuals that grew rapidly following metamorphosis, or individuals that emerged as large metamorphs, exerted the greatest influence on population growth rates. Large/fast-growing recruits are likely to breed in their first year. Evenness of elasticity values across the full IPM was low (EE = 0.34).

Despite parameterizing fecundity as size-dependent, the low survival of individuals to recruitment size, combined with the low probability of reaching maximum size, make size-specific differences in total reproductive value negligible (Figure 3). Stable size distribution for the population contained two cohorts (Figure 3), with one approximating the size of new recruits, suggesting that despite the longevity of flatwoods salamanders, most only experience one successful breeding event in their lifetime.

DISCUSSION

Three factors predispose flatwoods salamander populations to high risk of local extirpation; 1) they are small, 2) they experience stochastic recruitment, 3) they exhibit low elasticity evenness. Under a no-management scenario, populations have a 50% chance of persisting beyond 50 years. Management actions that achieve more consistent recruitment across years would drastically reduce extinction risk, but adult survival exhibits annual variability that can strongly influence long-term population growth.

Predicting the vulnerability of threatened and endangered species to extinction, and how future population trajectories may be affected by management interventions, is a primary objective of conservation biology (Clark et al., 2001, Wood 2018). Taxa with limited dispersal ability, including amphibians, reptiles, and small mammals, are especially susceptible to local extinction when habitat loss and degradation impede movement among local populations (Findlay & Houlahan 1997). Habitat loss and fragmentation are implicated in the decline of many amphibian species currently threatened with global extinction. Further, the low vagility of amphibians make them less likely to recolonize unoccupied sites following extirpation, often preventing a ‘hands-off’ approach to recovery (Waldman and McKinnon 1993, Blaustein et al. 1994).

Amphibians that breed in isolated wetlands require aquatic breeding habitat and terrestrial summer foraging habitat to persist (Regosin et al. 2003a, 2003b, Gibbons et al. 2006). The relative importance of aquatic vs. terrestrial habitat for population health is a topic of great contention (e.g.., Biek et al. 2002, Quesnelle et al. 2015), but clearly depends on the life-history of the species in question. Amphibians characterized with short life spans and high fecundities are most sensitive to wetland loss and isolation, whereas long-lived salamanders with comparatively small clutches are more strongly influenced by upland forest cover and terrestrial habitat degradation (Schmidt et al. 2005). Flatwoods salamanders appear to conform to theoretical expectations, and corroborate previous studies of archetypal long-lived vertebrates; whilst the stochastic nature of recruitment greatly exacerbates extinction risk, population growth rates are most sensitive to changes in adult survival (Crouse et al. 1987; Gaillard et al. 1998; Fujiwara & Caswell 2001, Schmidt et al. 2005).

Elasticity analysis involves identifying the life-history stage or vital rate that exerts the greatest impact on population growth (Norris 2004). Such methods should be used with caution however, as they make strong assumptions regarding how a population will respond to management (Pascual, Kareiva & Hillborn 1997; Ludwig 1999, Runge & Johnson 2002), and often extrapolate outside of the range of values used to construct the initial demographic model (Norris 2004). In addition, elasticity analyses do not consider the ability of management to manipulate vital rates, and thus do not always result in practical recommendations for conservation (Ehrlén, van Groenendael & de Kroon 2001). Elasticity analyses should not be conducted in a vacuum therefore, and instead the sensitivity of vital rates should be balanced with the feasibility of implementation (Mills et al. 1999, Norris 2004). The model presented here identifies stochastic recruitment and adult survival as the key components governing population growth, providing managers with a foundation from which to evaluate alternative management actions that target these components of the life-history. The unevenness exhibited in the elasticity scores across the IPM suggest a population unable to withstand much stochastic change, and indeed low evenness scores have been linked to imperilment status (Van Allen et al. 2012).

Temporal environmental variability can have negative effects on population viability by reducing the long-term growth rate of populations (Lewontin and Cohen 1969, Boyce et al. 2006). Environmental stochasticity generates most of the interannual variability in amphibian population growth rates by controlling recruitment success (Pechmann & Wilbur 1994; Pfister 1998; Biek et al. 2002). Worryingly, climate projections for the Southeastern US foreshadow an increase in recruitment failure with increasing aridity (Blaustein et al. 2001, 2010, Corn 2005, Shoo et al. 2011, Foden et al. 2013, Yiming et al. 2013). To combat these future concerns, various methods, all aimed at achieving more consistent recruitment, have become implemented in amphibian conservation with varying degrees of success. Captive rearing and *in situ* larval head-starting are by far the most common management activity (Griffiths and Pavajeau 2008), but can have disastrous consequences if the genetic ramifications of introductions are not carefully considered (Leberg and Firmin 2008). Alternatively, management can target the habitat to achieve more consistent recruitment; wetland hydrology can be manipulated and hydroperiod artificially extended through groundwater pumping, installation of pond liners, or upland stand thinning to reduce evapotranspiration rates (Seigel et al. 2006, Shoo et al. 2011, Jones et al. 2018). Although such measures would be predicted to have considerable impact (Figure 1), the cost of such management activities may preclude them as viable options (Seigel et al. 2006, Shoo et al. 2011). In addition, it is important to note that management actions achieving more consistent recruitment across years will yield an improvement in long-term population growth, but are unlikely to curb declines in isolation (Biek et al. 2002; Hels & Nachman 2002; Vonesh & De la Cruz 2002, Schmidt et al. 2005).

In contrast to recruitment (Shoop 1974, Schmidt et al. 2005, Middleton and Green 2015), adult survival appears comparatively stable in many taxa (Gaillard et al. 1998, Schmidt et al. 2005), and is thus much more likely to govern minimum population growth rates (Schmidt et al. 2005, Middleton and Green 2015); even a moderate reduction in adult survival has been shown to shift a population trajectory from stable to declining. As a rule, survival is expected to influence population viability more than recruitment, because survival dictates how long a population can persist in the absence of recruitment (Schmidt et al. 2005). Bet-hedging selects for high survival in populations that experience highly variable recruitment, even at the expense of reproductive output (Seger & Brockmann 1987, Schmidt et al. 2005). The surprising longevity of many caudates relative to their body size (Petranka 1998) alludes to such a bet-hedging strategy. Further, flatwoods salamanders exhibit a unique reproductive strategy whereby females scatter their eggs across dry wetland basins (Gorman et al. 2014), perhaps indicative of bet-hedging behavior *within* a breeding season.

Terrestrial habitat adjacent to wetlands is essential to the maintenance of wetland communities and thus alteration of terrestrial habitat by human land-use can cause declines and local extinctions of wetland-dependent organisms (Means et al. 1996; Findlay & Houlahan 1997; Calhoun & Klemens 2002). Population declines can occur as a result of direct mortality from human activities or from habitat loss and degradation that act to reduce annual survival rates (Gibbs 1998). Local extinctions may also occur when land-use isolates small populations, preventing immigration and recolonization (Gibbs 2000). An analysis of data from the literature on 32 amphibian species suggests that core terrestrial habitat (the area encompassing 95% of the adults in a population) extends on average 159–290 m from breeding wetlands (Semlitsch & Bodie 2003). Results of several other studies show that adult amphibians regularly use terrestrial habitat as far away as 1 km or more from the breeding sites (reviewed in Patrick et al. 2006).

Historically, amphibian conservation efforts have centered around breeding habitats, larval recruitment, and wetland restoration (Marsh and Trenham 2001). Even for fully aquatic species however, landscape variables associated with the surrounding terrestrial environment are important determinants of population viability (Vos and Chardon 1998, Marsh and Trenham 2001, Denoël and Ficetola 2008, Veysey et al. 2011, Quesnelle et al. 2015). Adult survival is much higher in forested uplands surrounding breeding wetlands compared with sites that have been clearcut (Houlahan and Findlay 2003, Rubbo and Kiesecker 2005, Denoël and Ficetola 2008), or that feature roads and urban development (Vos and Chardon 1998, Pillsbury and Miller 2008, Veysey et al. 2011). As more of the upland matrix surrounding breeding wetlands becomes fragmented and degraded, journeys between wetlands will become harsher, successful migration events will become rarer, and the rate of recolonization/rescue severely reduced (Travis 1994, Todd et al. 2014). Diagnosing the apparent low survival estimates of flatwoods salamanders compared to congeners, and identifying the primary sources of adult mortality, should be a research priority. For amphibian conservation to be effective, management must adopt a landscape-scale approach that considers all stages of the species' life history (Schmidt et al. 2005, Middleton and Green 2015, Quesnelle et al. 2015).

Despite the broad utility of demographic modelling, less than a quarter of recovery plans for threatened and endangered amphibians in the USA contain steps to develop and conduct a population viability analysis (Morris et al. 2002, Norris 2004). The quantity and quality of data required to construct useful demographic models is lacking for virtually all amphibian species (Schmidt et al.2005). Even for relatively well studied species, data across all stages of the amphibian life-cycle are rarely collected (Biek et al. 2002; Vonesh & De la Cruz 2002, Schmidt et al. 2002, 2005). Given the challenge in parsing out natural fluctuations from population declines in many amphibian taxa (Chesson and Warner 1981, Pechmann et al. 1991, Dodd 1993, Semlitsch et al. 1996, Vucetich and Waite 1998, Alford and Richards 1999, Whiteman and Wissinger 2005, Salvidio 2009), it seems surprising that long-term studies designed to obtain the demographic data required for projection models do not occupy a more prominent position in amphibian conservation.

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LITERATURE CITED

Akçakaya, H.R., and Sjögren-Gulve, P. 2000. Population viability analyses in conservation planning: an overview. Ecological Bulletins, 9-21.

Alford, R.A., and Richards, S.J. 1999. Global amphibian declines: a problem in applied ecology. Annual Reviews of Ecology and Systematics, 30:133–165.

Anderson J.D., and Williamson, G.K. 1976. Terrestrial mode of reproduction in *Ambystoma cingulatum*. Herpetologica, 32:214-221.

Bakker, V.J., and Doak, D.F. 2009. Population viability management: ecological standards to guide adaptive management for rare species. Frontiers in Ecology and the Environment, 7:158-165.

Beissinger, S.R., and McCullough, D.R. 2002. Population viability analysis. University of Chicago Press.

Bell, T.J., Powell, K.I., and Bowles, M.L. 2013. Viability model choice affects projection accuracy and reintroduction decisions. The Journal of Wildlife Management, 77:1104-1113.

Biek, R., Funk, W.C., Maxell, B.A., and Mills, L.S. 2002. What is missing in amphibian decline research: insights from ecological sensitivity analysis. Conservation Biology, 16:728-734.

Blaustein, A.R., Wake, D.B., and Sousa, W.P. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. Conservation Biology, 8:60-71.

Boone, M. D., and Bridges, C.M. 2003. Effects of pesticides on amphibian populations. Pp. 152–167 in R.D. Semlitsch, editor. Amphibian conservation. Smithsonian Institution Press, Washington, D.C.

Boyce, M.S., Haridas, C.V., Lee, C.T., and NCEAS Stochastic Demography Working Group. 2006. Demography in an increasingly variable world. Trends in Ecology and Evolution, 21:141-148.

Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akcakaya, R., and Frankham R. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature, 404:385-387.

Brook, B.W., Burgman, M.A., Akçakaya, H.R., O'grady, J.J. and Frankham, R. 2002. Critiques of PVA ask the wrong questions: throwing the heuristic baby out with the numerical bath water. Conservation Biology, 16:262-263.

Calhoun, A.J.K., and Klemens, M.W. 2002. Best development practices for conserving pool-breeding amphibians. Wildlife Conservation Society Technical Paper 5.

Caswell, H. 2001. Matrix population models: Construction, analysis, and interpretation. Sunderland, Mass, Sinauer Associates.

Caswell, H., de Vries, C., Hartemink, N., Roth, G. and van Daalen, S.F. 2018. Age× stage-classified demographic analysis: a comprehensive approach. Ecological Monographs, 88:560-584.

Chamberlin, T.C. 1965. The method of multiple working hypotheses. Science, 754-759.

Chesson, P. L., and Warner, R.R. 1981. Environmental variability promotes coexistence in lottery competitive systems. American Naturalist, 117:923-943.

Childs, D.Z., Rees, M., Rose, K.E., Grubb, P.J., and Ellner, S.P. 2004. Evolution of size-dependent flowering in a variable environment: Construction and analysis of a stochastic integral projection model. Proceedings of the Royal Society B: Biological Science, 271:425-434.

Clark, J.S., Carpenter, S.R., Barber, M., Collins, S., Dobson, A., Foley, J.A., Lodge, D.M., Pascual, M., Pielke, R., Pizer, W., Pringle, C., Reid, W.V., Rose, K.A., Sala, O., Schlesinger, W.H., Wall, D.H., and Pringle, C. 2001. Ecological forecasts: an emerging imperative. Science, 293:657–660.

Coale, A.J. 1972. The growth and structure of human populations: a mathematical approach. Princeton University Press, Princeton, New Jersey, USA.

Cole, L.C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology, 29:103– 137.

Collins, J. P., and Storfer, A. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distributions, 9:89–98.

Coulson, T., Mace, G.M., Hudson, E., and Possingham, H. 2001. The use and abuse of population viability analysis. Trends in Ecology and Evolution, 16:219-221.

Coulson, T. 2012. Integral projections models, their construction and use in posing hypotheses in ecology. Oikos, 121:1337-1350.

Crouse, D.T., Crowder, L.B., and Caswell, H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology, 68:1412–1423.

Deevey, E.S. 1947. Life tables for natural populations of animals. Quarterly Review of Biology, 22:283-314.

Denoël, M., and Ficetola, G.F. 2008. Conservation of newt guilds in an agricultural landscape of Belgium: the importance of aquatic and terrestrial habitats. Aquatic Conservation: Marine and Freshwater Ecosystems, 18:714–728.

Easterling, M.R., Ellner, S.P., and Dixon, P.M. 2000. Size-specific sensitivity: Applying a new structured population model. Ecology, 81:694-708.

Ehrlén, J., van Groenendael, J., and de Kroon, H. 2001. Reliability of elasticity analysis: reply to Mills et al. Conservation Biology, 15:278–280.

Ellner, S.P., Fieberg, J., Ludwig, D., and Wilcox, C. 2002. Precision of population viability analysis. Conservation Biology, 16:258-261.

Ellner, S.P., and Rees, M. 2007. Stochastic stable population growth in integral projection models: theory and application. Journal of Mathematical Biology, 54:227-256.

Ellner, S.P., Childs, D.Z., and Rees, M. 2016. Data-driven modelling of structured populations. Springer, New York, New York, USA.

Enright, N.J., Franco, M., and Silvertown, J. 1995. Comparing plant life histories using elasticity analysis: The importance of life span and the number of life-cycle stages. Oecologia, 104:79-84.

Fieberg, J., and Ellner, S.P. 2000. When is it meaningful to estimate an extinction probability? Ecology, 81:2040-2047.

Findlay, C.S., and Houlahan, J. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. Conservation Biology, 11:1000-1009.

Forbes, V.E., and Calow, P. 2002. Population growth rate as a basis for ecological risk assessment of toxic chemicals. Philosophical Transactions of the Royal Society of London, Biological Sciences, 357:1299-1306.

Fujiwara, M., and Caswell, H. 2001. Demography of the endangered north Atlantic right whale. Nature, 414:537–541.

Gaillard, J.M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution, 13:58–63.

García-Díaz, P., Prowse, T.A., Anderson, D.P., Lurgi, M., Binny, R.N., and Cassey, P. 2019. A concise guide to developing and using quantitative models in conservation management. Conservation Science and Practice, 1:11.

Gibbons, J.W., Winne, C.T., Scott, D.E., Willson, J.D., Glaudas, X., Andrews, K.M., Todd, B.D., Fedewa, L.A., Wilkinson, L., Tsaliagos, R.N., and Harper, S.J. 2006. Remarkable amphibian biomass and abundance in an isolated wetland: implications for wetland conservation. Conservation Biology, 20:1457-1465.

Gibbs, J.P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. The Journal of Wildlife Management, 584-589.

Gibbs, J.P. 2000. Wetland loss and biodiversity conservation. Conservation Biology, 14:314-317.

Goin, C.J. 1950. A study of the salamander, *Ambystoma cingulatum*, with the description of a new subspecies. Annals of the Carnegie Museum of Natural History, 31:299-321.

Gorman, T.A., Powell, S.D., Jones, K.C., and Haas, C.A. 2014. Microhabitat characteristics of egg deposition sites used by reticulated flatwoods salamanders. Herpetological Conservation and Biology, 9:543-550.

Green, A.W., and Bailey, L.L., 2015. Using Bayesian population viability analysis to define relevant conservation objectives. PloS One, 10:e0144786.

Griffiths, R.A., and Pavajeau, L. 2008. Captive breeding, reintroduction, and the conservation of amphibians. Conservation Biology, 22:852-861.

Halley, J.M., Oldham, R.S., and Arntzen, J.W. 1996. Predicting the persistence of amphibian populations with the help of a spatial model. Journal of Applied Ecology, 33:455–470.

Harper, E.B., Rittenhouse, T.A., and Semlitsch, R.D. 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.

Hels, T., and Nachman, G. 2002. Simulating viability of a spadefoot toad *Pelobates fuscus* metapopulation in a landscape fragmented by a road. Ecography, 25:730–744.

Heppell, S.S., Caswell, H, and Crowder, L.B. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology, 81:654–665.

Himes Boor, G.K. 2014. A framework for developing objective and measurable recovery criteria for threatened and endangered species. Conservation Biology, 28:33-43.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., and Kuzmin, S.L. 2000. Quantitative evidence for global amphibian population declines. Nature, 404:752–755.

Houlahan, J.E., and Findlay, C.S. 2003. The effects of adjacent land use on wetland amphibian species richness and community composition. Canadian Journal of Fisheries and Aquatic Sciences, 60:1078–1094.

Jäkäläniemi, A., Postila, H., and Tuomi, J, 2013. Accuracy of short-term demographic data in projecting long-term fate of populations. Conservation Biology, 27:552-559.

Jones, C.N., McLaughlin, D.L., Henson, K., Kaplan, D.A., and Haas, C.A. 2018. From salamanders to greenhouse gasses: Does upland management affect wetland function? Frontiers in Ecology and the Environment, 16:14-19.

Kiesecker, J.M., Blaustein, A.R., and Belden, L.K. 2001. Complex causes of amphibian declines. Nature, 410:681–684.

Leberg, P.L., and Firmin, B.D. 2008. Role of inbreeding depression and purging in captive breeding and restoration programmes. Molecular Ecology, 17:334–343.

Lefkovitch, L. 1965. The study of population growth in organisms grouped by stages. Biometrics, 21:1-18.

Leslie, P.H. 1945. On the use of matrices in certain population mathematics. Biometrika, 33:183-212.

Leslie, P. H., and Park, T. 1949. The intrinsic rate of natural increase of *Tribolium castaneum*. Ecology, 30: 469-477.

Lewontin, R.C., and Cohen, D. 1969. On population growth in a randomly varying environment. Proceedings of the National Academy of sciences, 62:1056-1060.

Lotka, A.J. 1939. Analytical theory of biological populations. Translated by D. P. Smith and H. Rossert. Plenum Press, New York, NY.

Lotts, K.C., Waite, T.A., and Vucetich, J.A. 2004. Reliability of absolute and relative predictions of population persistence based on time series. Conservation Biology, 18:1224-1232.

Ludwig, D. 1996. Uncertainty and the assessment of extinction probabilities. Ecological Applications, 6:1067–1076.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? Ecology, 80: 298–310.

Malthus, T.R. 1872. An essay on the principle of population.

Marsh, D.M., and Trenham, P.C. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology, 15:40-49.

McCarthy, M.A., Andelman, S.J., and Possingham, H.P. 2003. Reliability of relative predictions in population viability analysis. Conservation Biology, 17:982–989.

Means, D.B., Palis, J.G., and Baggett, M. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander. Conservation Biology, 10:426-437.

Merow, C., Dahlgren, J.P., Metcalf, C.J.E., Childs, D.Z., Evans, M.E.K., Jongejans, E., Record, S., Rees, M., Salguero-Gómez, R., and McMahon, S.M. 2014. Advancing population ecology with integral projection models: A practical guide. Methods in Ecology and Evolution, 5:99-110.

Middleton, J., and Green, D.M. 2015. Adult age-structure variability in an amphibian in relation to population decline. Herpetologica, 71:190-195.

Mills, L.S., Doak, D.F., and Wisdom, M.J. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology, 13:815–829.

Morris, W.F., Bloch, P.L., Hudgens, B.R., Moyle, L.C., and Stinchcombe, J.R. 2002. Population viability analysis in endangered species recovery plans: past use and future improvements. Ecological Applications, 12:708-712.

Morrison, C., Wardle, C., and Castley, J.G. 2016. Repeatability and reproducibility of population viability analysis (PVA) and the implications for threatened species management. Frontiers in Ecology and Evolution, 4:98.

Nisbet, R.M., and Gurney, W. 1982. Modelling fluctuating populations. Wiley, Chichester, UK.

Norris, K.E.N. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. Journal of Applied Ecology, 41:413-426.

Oppel, S., Hilton, G., Ratcliffe, N., Fenton, C., Daley, J., Gray, G., Vickery, J., and Gibbons, D. 2014. Assessing population viability while accounting for demographic and environmental uncertainty. Ecology, 95:1809-1818.

Pascual, M.A., Kareiva, P., and Hillborn, R. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. Conservation Biology, 11:966–976.

Patrick, D.A., Hunter Jr, M.L., and Calhoun, A.J. 2006. Effects of experimental forestry treatments on a Maine amphibian community. Forest Ecology and Management, 234:323-332.

Patterson, B.R., and Murray, D.L. 2008. Flawed population viability analysis can result in misleading population assessment: a case study for wolves in Algonquin park, Canada. Biological Conservation, 141:669-680.

Pechmann, J.H.K, Scott, D.E., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J., and Gibbons, W. 1991. Declining amphibian populations: The problem of separating human impacts from natural populations. Science, 253:892-895.

Pechmann, J.H.K., and Wilbur, H.M. 1994. Putting declining amphibian populations in perspective: natural fluctuations and human impacts. Herpetologica, 50:65–84.

Pfister, C.A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences, 95:213–218.

Pillsbury, F.C., and Miller, J.R. 2008. Habitat and landscape characteristics underlying anuran community structure along an urban–rural gradient. Ecological Applications, 18:1107–1118.

Platt, J.R. 1964. Strong inference. Science, 146:347-353.

Quesnelle, P.E., Lindsay, K.E., and Fahrig, L. 2015. Relative effects of landscape-scale wetland amount and landscape matrix quality on wetland vertebrates: a meta-analysis. Ecological Applications, 25:812-825.

R Core Team. 2018. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Ramula, S., and Lehtilä, K. 2005. Matrix dimensionality in demographic analyses of plants: when to use smaller matrices?. Oikos, 111:563-573.

Rees, M., and Ellner, S.P. 2009. Integral projection models for populations in temporally varying environments. Ecological Monographs, 79:575–594.

Rees, M., Childs, D.Z., and Ellner, S.P. 2014. Building integral projection models: A user's guide. The Journal of Animal Ecology, 83:528-545.

Rubbo, M.J., and Kiesecker, J.M. 2005. Amphibian breeding distribution in an urbanized landscape. Conservation Biology, 19:504–511.

Runge, M.C., and Johnson, F.A. 2002. The importance of functional form in optimal control solutions of problems in population dynamics. Ecology, 83:1357–1371.

Salguero-Gómez, R. 2015. The COMPADRE plant matrix database: an open online repository for plant demography. Journal of Ecology, 103:202-218.

Salguero-Gómez, R. 2016. COMADRE: a global data base of animal demography. Journal of Animal Ecology, 85:371-384.

Salvidio, S. 2009. Detecting amphibian population cycles: the importance of appropriate statistical analyses. Biological Conservation, 142:455-461.

Schmidt, B.R., Schaub, M., and Anholt, B.R. 2002. Why you should use capture-recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration, overdispersion, and common toads. Amphibia-Reptilia, 23:375–388.

Schmidt, B.R., Feldmann, R., and Schaub, M. 2005. Demographic processes underlying population growth and decline in *Salamandra salamandra*. Conservation Biology, 19:1149-1156.

Seger, J., and Brockmann, H.J. 1987. What is bet-hedging? Oxford Surveys in Evolutionary Biology, 4:182–211.

Seigel, R.A., Dinsmore, A., and Richter, S.C. 2006. Using well water to increase hydroperiod as a management option for pond-breeding amphibians. Wildlife Society Bulletin, 34:1022–1027.

Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., and Gibbons, J.W. 1996. Structure and dynamics of an amphibian community. pp.217-248 in C.L. Martin (eds) Long-term studies of vertebrate communities, Academic Press.

Semlitsch, R.D. 2003. Conservation of pond-breeding amphibians. Pp. 8–23 in R.D. Semlitsch, (eds), Amphibian conservation. Smithsonian Institution Press, Washington, D.C.

Semlitsch, R.D., and Bodie, J.R. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology, 17:1219-1228.

Shoo, L.P., Olson, D.H., McMenamin, S.K., Murray, K.A., Van Sluys, M., Donnelly, M.A., Stratford, D., Terhivuo, J., Merino-Viteri, A., Herbert, S.M., and Bishop, P.J. 2011. Engineering a future for amphibians under climate change. Journal of Applied Ecology, 48:487-492.

Shoop, C.R. 1974. Yearly variation in larval survival of *Ambystoma maculatum*. Ecology, 55:440–444.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Taylor, B.L. 1995. The reliability of using population viability analysis for risk classification of species. Conservation Biology, 9:551–558.

Taylor, B.E., and Scott, D.E. 1997. Effects of larval density dependence on population dynamics of *Ambystoma opacum*. Herpetologica, 53:132–145.

Todd, B.D., Blomquist, S.M., Harper, E.B., and Osbourn, M.S. 2014. Effects of timber harvesting on terrestrial survival of pond-breeding amphibians. Forest Ecology and Management, 313:123–131.

Travis, J. 1994. Calibrating our expectations in studying amphibian populations. Herpetologica, 50:104-108.

Tuljapurkar, S. 1990. Population dynamics in variable environments. Springer-Verlag, New York, New York, USA.

Ureta, C., Martorell, C., Hortal, J., and Fornoni, J. 2012. Assessing extinction risks under the combined effects of climate change and human disturbance through the analysis of life-history plasticity. Perspectives in Plant Ecology, Evolution and Systematics, 14:393-401.

Van Allen, B.G., Dunham, A.E., Asquith, C.M., and Rudolf, V.H.W. 2012. Life history predicts risk of species decline in a stochastic world. Proceedings of the Royal Society B: Biological Science, 279:2691–2697.

van Poorten, B.T., Beck, M., and Herborg, L.M. 2019. Turning population viability analysis on its head: using stochastic models to evaluate invasive species control strategies. Biological Invasions, 21:1197-1213.

Veysey, J.S., Mattfeldt, S.D., and Babbitt, K.J. 2011. Comparative influence of isolation, landscape, and wetland characteristics on egg-mass abundance of two pool-breeding amphibian species. Landscape Ecology, 26:661–672.

Vindenes, Y., Engen, S., and Saether, B.E. 2011. Integral projection models for finite populations in a stochastic environment. Ecology, 92:1146–1156.

Vonesh, J.R., and De la Cruz, O. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia, 133:325-333.

Vos, C.C., and Chardon, J.P. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. Journal of Applied Ecology, 35:44–56.

Vucetich, J.A., and Waite, T.A. 1998. Number of censuses required for demographic estimation of effective population size. Conservation Biology, 12:1023-1030.

Weiss-Lehman, C., Davies, K.F., Clements, C., and Melbourne, B.A. 2017. Estimating extinction risk with minimal data. Biological Conservation, 213:194-202.

Whiteman, H.H., and Wissinger, S.A. 2005. Amphibian population cycles and long-term data sets. pp. 177–184 In Lannoo, M.L. (eds), Amphibian declines: Conservation status of United States species. California University Press, Berkeley.

Wilbur, H.M. 1980. Complex life cycles. Annual Reviews of Ecology and Systematics, 11:67–93.

Wilbur, H.M., and Collins, J.P. 1973. Ecological aspects of amphibian metamorphosis. Science, 182:1305–1314.

Wood, K.A., Stillman, R.A., and Hilton, G.M. 2018. Conservation in a changing world needs predictive models. Animal Conservation, 21:87-88.

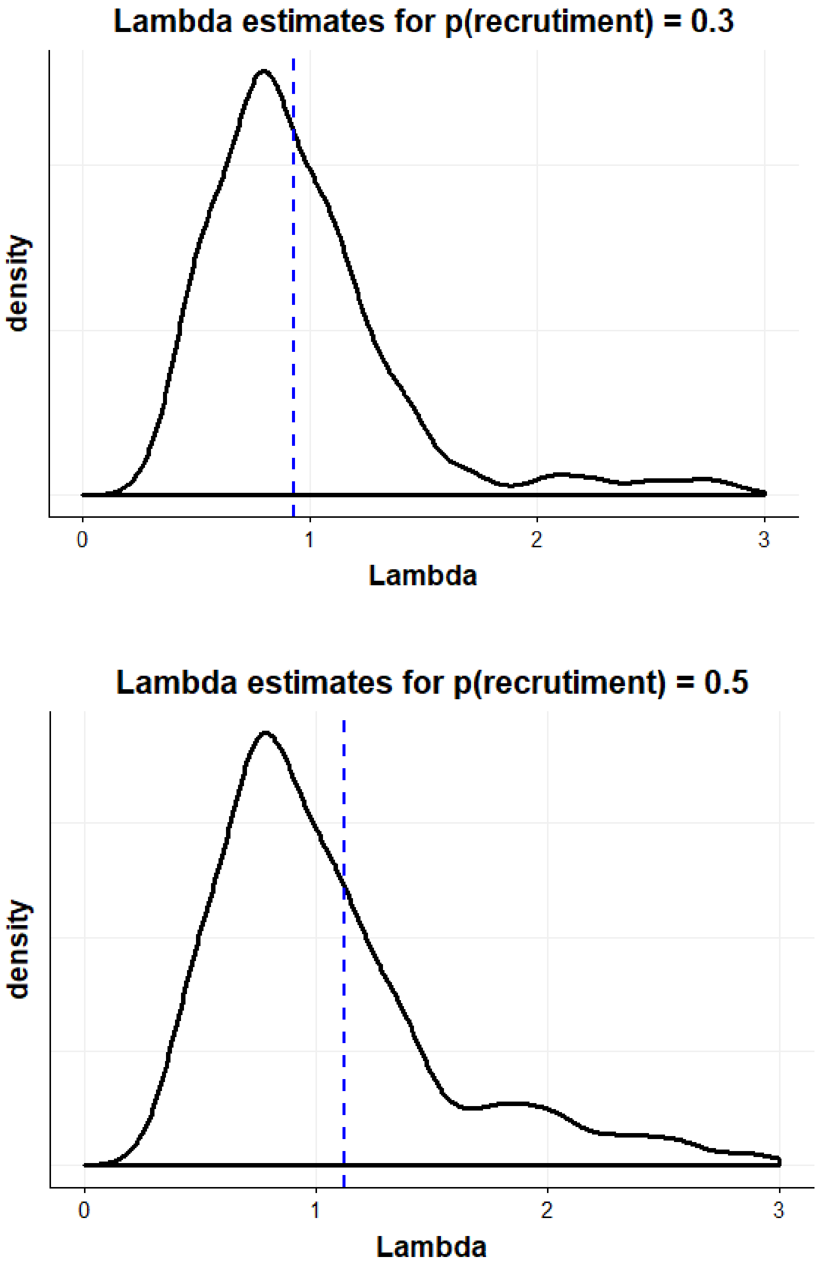

Figure 1. Uncertainty in predicted long term population growth rate (lambda) obtained from 1000 forward projections for scenarios when probability of recruitment equals 30% and 50% respectively. Dashed lines reflect the posterior medians.

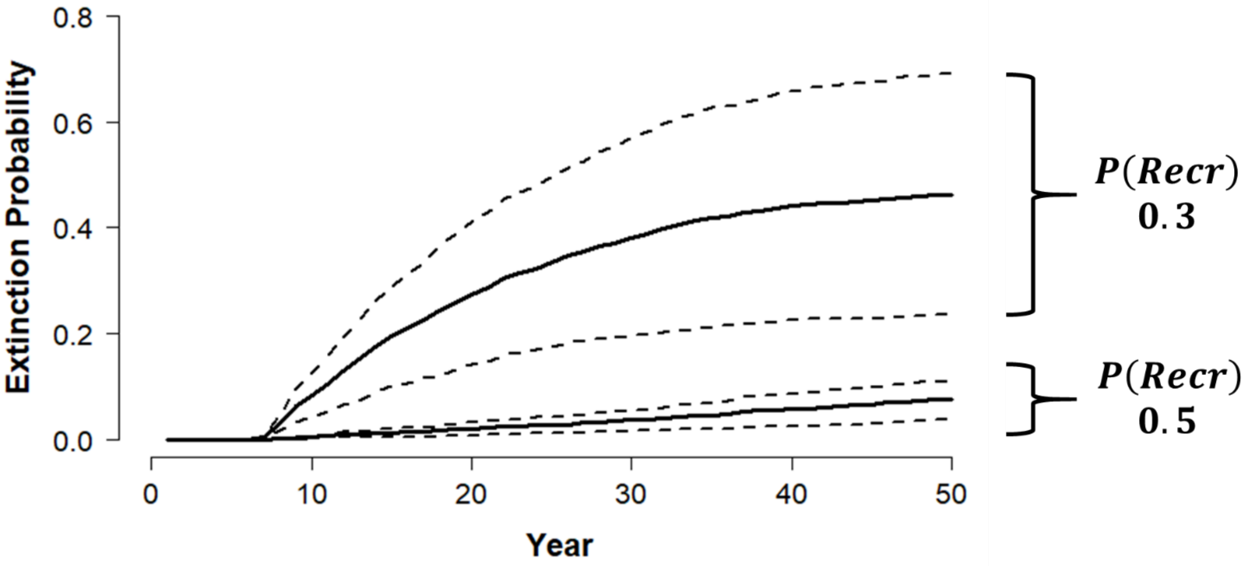

Figure 2. Extinction probabilities for populations of reticulated flatwoods salamanders. Scenarios presented represent successful recruitment on average every three years (0.3) and every two years (0.5). Solid lines reflect posterior means, and dashed lines represent 95% credible intervals derived from 1000 simulations.

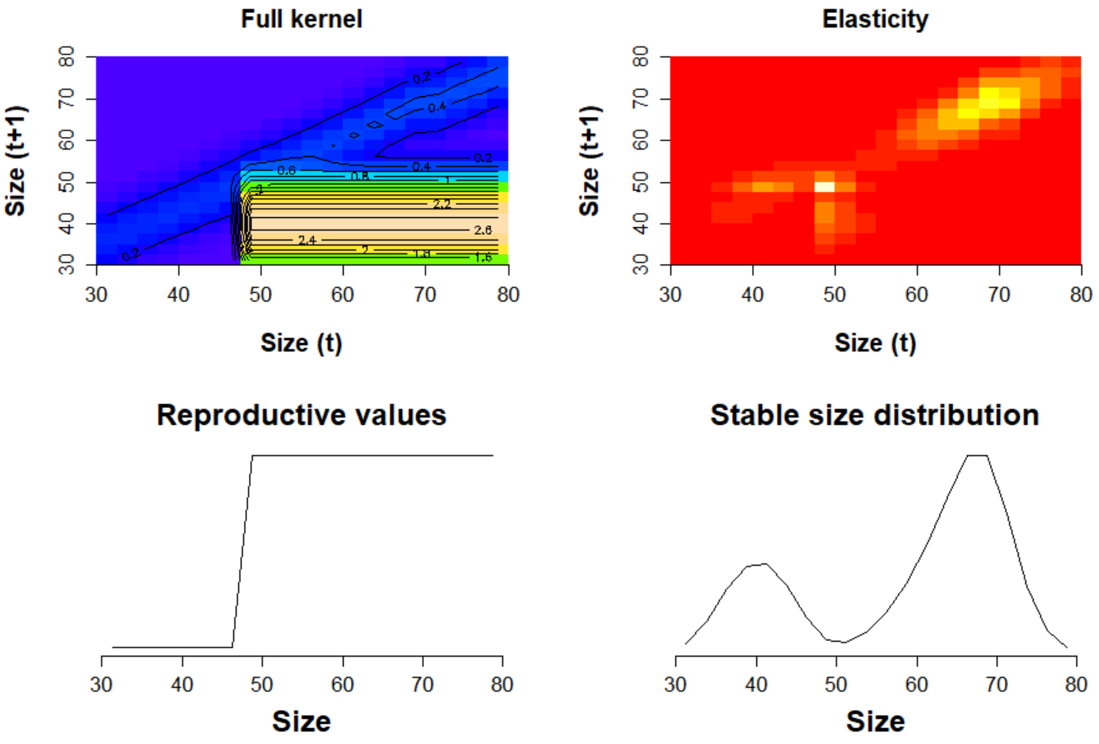

Figure 3. a) Visual representation of the full IPM kernel for reticulated flatwoods salamanders, b) elasticity analysis of the full IPM kernel where white/yellow indicates the highest change in population growth with the corresponding change in vital rate; c) the effect of body size on relative reproductive value, and d) the stable size distribution. Size reflects snout-vent length (SVL) in mm.

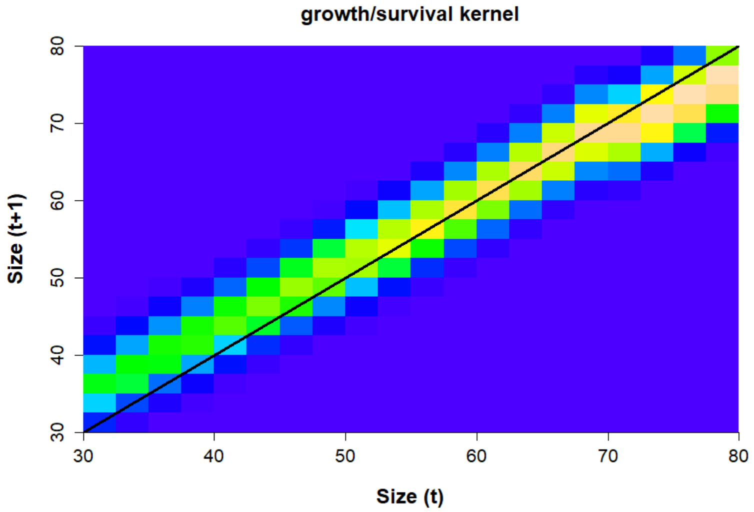

Figure 4. The survival/growth kernel from the final IPM, plotted separately for ease of visualization. Light colors represent areas of high density. Size is measured as snout-vent length (SVL) in mm.

CONCLUDING REMARKS

Amphibian Demography and Conservation

Demographic models have become a centerpiece in the management of threatened and endangered species (Beissinger & Westphal 1998; Beissinger & McCulloch 2002). Models range in complexity, but typically amalgamate vital rates associated with different life history traits or stages to predict population size, future population growth, and ultimately extinction risk (Mace & Lande 1991, Norris 2004). Further, demographic models can be used to guide the conservation of imperiled species and evaluate a range of management scenarios, by identifying components of the life-history that exert the greatest influence on population growth (Beissinger & Westphal 1998, Benton & Grant 1999; Beissinger & McCulloch 2002; Reed et al. 2002). Owing to the theoretical underpinnings of demographic models, results are readily generalizable, and can be used to make inferences for data-poor species with similar life-histories (Biek et al. 2002).

Many pond-breeding amphibians exhibit marked fluctuations in abundance through time (Semlitsch 1983, 1987, Berven 1990, Pechmann et al. 1991, Semlitsch et al. 1996, 2014, Whiteman and Wissinger 2005, Taylor et al. 2006), requiring long time-series to discern real trends from stochastic noise. Demographic models constructed from long-term datasets yield novel insights into a species' life-history that can help tailor management efforts (Heppell et al. 2000, Biek et al. 2002). Notwithstanding common issues associated with the implementation of ecological modelling (Getz et al. 2018), the uncertainty of inferences from demographic projections concerning population trends is an order-of-magnitude less than concomitant extinction rate estimates (Balmford et al.

2003). Indeed, even simple models constructed from a paucity of data harbor real conservation value.

Throughout this thesis, we have adopted a Bayesian methodology. Historically, there was a strong tendency to debate Bayesian vs. frequentist approaches from either a philosophical or ideological standpoint. In the 21st century however, the superiority of Bayesian methods is a well demonstrated fact (Jaynes 2003). In particular, we adopted a Bayesian approach to easily account for multiple sources of uncertainty, model hierarchical relationships, and include prior knowledge (with varying levels of confidence) concerning parameters of interest (Gelman et al. 2013). Bayesian methods also more accurately reflect the iterative, cumulative nature of scientific advances; today's predictions will be tomorrows priors. Given the hodgepodge nature of ecological datasets, and the hierarchical nature of ecological processes, Bayesian methods will only grow in popularity.

Amphibian Life Histories and Conservation

The life-histories of ectotherms are much more influenced by environment than equivalent endotherm species (Shine 2005). Indeed, flexibility in the allocation of resources between various life-processes appears to be selected for in pond-breeding amphibians (Maiorana 1976, Shine 2005). Stochastic forces that disproportionately affect small individuals act to generate a life history that does not fall neatly into any of the classic strategies (Pianka 1970, Grime 1977, Winemiller 2005). Instead, the environmental unpredictability associated with ephemeral wetlands has resulted in species with the ability to quickly divert resources to reproduction when conditions are favorable and the ability to persist on the landscape during long periods of drought (Fretwell 1972).

Demographic models confirm the importance of post-metamorphic mortality in driving the local dynamics of amphibian populations (Biek et al. 2002, Vonesh and de la Cruz 2002, Salice et al. 2011). In hindsight it is not surprising that, particularly for long-lived species that spend a disproportionate amount of the life-history in the terrestrial form, forest amount and upland quality exert a greater influence on amphibian abundance than wetland density. Nevertheless, as has been shown in other amphibians (Hatfield et al. 2004), low larval survival and catastrophes place a premium on early female maturity. Salamanders, it appears, exhibit a mixture of periodic and opportunistic strategies (Winemiller 2005).

When scaling up from individual vital rates to infer population dynamics, it is essential that conservation assessments separate agents of decline from factors that increase the risk of stochastic extirpation, i.e. the declining vs. the small population paradigms (Caughley 1994), because goals for recovery will likely differ from those of crisis prevention. Clearly the primary agent of decline for flatwoods salamanders is habitat loss. The wholesale reduction of longleaf pine ecosystems to less than 3% of their former range has resulted in the precipitous decline of entire communities that once inhabited these forests (Ware et al. 1993, Noss et al. 1995, Van Lear et al. 2005, Frost 2007, Hoctor et al. 2007). Clearly, restoration of longleaf to its historical extent should be the broad, long-term objective of conservation efforts in the southeastern US, but populations in remnant forest fragments face more immediate threats to persistence than continued habitat destruction.

Stochastic forces pose disproportionate risks to small and isolated populations (Goodman 1987, Lande 1993, Green 2003, Salvidio 2009), and thus are of salient concern for species on the brink of extinction. Owing to the vagaries of history, obligate longleaf pine species are now restricted to small and isolated patches. Hence, in the interim before widespread reforestation efforts commence, it seems prudent to attempt to stabilize relictual populations by mitigating the threats outlined in the small-population paradigm (Caughley 1994).

Amphibian Prospects and Conservation

The age of amphibians drew to a close almost 300 million years ago, as the late Carboniferous ushered in a new era of reptilian supremacy. Notwithstanding their fall from dominance, increasing competition stemming from the radiations of terrestrial vertebrate groups, and three mass extinction events, amphibians endure. Despite this apparent resiliency, novel anthropogenic pressures are raising legitimate concerns as to the continued persistence of amphibian taxa; time may be running out for this clade (Vitt et al. 1990, Stuart et al. 2004; Wake and Vredenburg, 2008). Indeed, the fate of amphibians may be already sealed; it has been suggested that our inability to curb global amphibian declines may reflect the scale of the extinction debt amphibians are currently experiencing (Hanski et al. 1996, Blaustein et al. 2010, Semlitsch et al. 2017).

Perhaps stemming from the current trajectory of many amphibian populations, they are often touted as great bioindicators; barometers of ecosystem health that can be used as early warning systems for habitat degradation. Despite frequent declarations to the contrary (e.g., Vitt et al. 1990), amphibians do not meet many of the published criteria of bioindicators however (Sewell and Griffiths 2009), and their use as such has rarely been empirically evaluated. Further, to frame species in bioindicator terms creates a false perception of amphibians amongst the public as weak/inferior animals that are insufficiently equipped to cope with the pace of global change. Conservation initiatives are seldom likely to succeed without staunch public support (e.g., Carroll et al. 2001), and a ‘canary in the coalmine’ portrayal of amphibians conveys an unnecessarily defeatist attitude.

Here we advocate for a more positive approach towards amphibian conservation that champions the values they provide when still extant. The keystone species concept provides an alluring alternative, not only because it yields simple conservation actions, but because it also reveals information on ecosystem functioning (Simberloff 1998). Several salamanders have been proposed as keystone species because of the role they play in maintaining a diverse aquatic invertebrate community (Davic 1984, Fauth 1999). The use of the concept as a broad conservation tool is limited however, because the identity of keystone species varies geographically, even in very similar systems (Power et al. 1996, Fauth 1999).

Of all the surrogate-species approaches to conservation, the umbrella species concept has gained the most traction, owing to its simplicity and practicality of implementation (Caro and O’Doherty 1999, Caro 2010). By directing conservation efforts toward species with the most exigent requirements, one is likely to confer protection to many co-occurring species (Frankel and Soule 1981, Roberge and Angelstam 2004). Despite a notable lack of empirical validation (Caro & O'Doherty 1999; Fleishman et al. 2001), the umbrella species concept offers an appealing shortcut for wildlife management (Branton and Richardson 2010, Li and Pimm 2016). Umbrella species can be used to determine the minimum size for protected areas and to set the minimum standards for ecosystem composition and structure (Launer and Murphy 1994).

Selection of candidate umbrella species has largely been restricted to area-based criteria, and as such most suggested umbrella species to date are large mammals and wide-ranging birds (Eisenberg 1980, Berger 1997, Fleury et al. 1998, Suter et al. 2002, but see Launer and Murphy 1994, New 1997). The umbrella species concept has been extended to include other criteria for consideration, such as habitat requirements and landscape connectivity (Fleury et al. 1998, van Langevelde et al. 2000, Ozaki et al. 2006, Roberge et al. 2008, Seddon & Leech 2008). For example, specialists are theorized to function as better umbrellas than generalist species (Ozaki et al. 2006; Roberge et al. 2008), provided the organism not be so specialized as to preclude benefits to other species as a result of conservation actions (Seddon and Leech 2008).

There has been a call for more assessment of potential umbrella species from underrepresented taxa, particularly amphibians (Bauer et al. 2010, Branton and Richardson 2010). Here we argue that amphibians are excellent candidates for umbrella species status. Because most amphibians require both aquatic and terrestrial habitats to complete their life-cycles (Duellman and Trueb 1986), both aquatic and terrestrial communities will fall under the umbrella’s protective reach. Further, many amphibians are poor dispersers with high site fidelity; managing the landscape at the scale of amphibian dispersal will provide ample connectivity for more vagile species. In a meta-analysis of African communities, amphibian umbrella species performed equally well to mammals (Rondinini and Boitani 2006).

Many amphibians are thought to exist in metapopulations however, and thus at any one time there will be a proportion of suitable patches unoccupied, in addition to some transient sink populations (Hanski 1999, Watson et al. 2001). Without long-term data therefore, it is challenging to assess the viability of populations supposedly acting as a bellwether for community health. Accounting for the dynamic properties of amphibian populations is equally important for designating critical habitat and including all necessary patches in a conservation network (Roberge and Angelstam 2004).

Combining umbrella species, to cover the broadest array of limiting factors to which a community is subjected, offers the most exciting avenue for application of this concept (Lambeck 1997). Lambeck's ‘focal’ species approach involves identifying threats and targeting management at species most sensitive to those threats. It is Gause’s law in reverse, whereby we care not about the winners of competition for a limiting resource, but the losers. Anthropogenic threats create new limiting factors, new arenas for competition that are won by species insensitive to those limits. Consider an ecosystem threatened primarily by habitat loss and fragmentation. Such landscape changes would provide a competitive edge to species that are not limited by patch area or dispersal ability, and thus only those taxa would persist. A combined management approach for two ‘focal’ species, one that has large area requirements and one with low vagility, would confer adequate protection for most members of the wider community (Lambeck 1997, Watson et al. 2001).

In summary, amphibian conservation would benefit from 1) an increase in systematic, long-term data collection for parameterizing demographic models, 2) greater utilization of life-history theory to draw inference for understudied species. Further, conservation must account for the social milieu that surrounds conservation activities to be effective, and thus improved perceptions of amphibian taxa amongst the public will be crucial. With tremendous collective effort, and perhaps some luck, the fate of amphibians may not be the foregone conclusion some people fear.

LITERATURE CITED

Balmford, A., Green, R.E., and Jenkins, M. 2003. Measuring the changing state of nature. Trends in Ecology & Evolution, 18:326-330.

Bauer, D.M., Paton, P.W., and Swallow, S.K. 2010. Are wetland regulations cost effective for species protection? A case study of amphibian metapopulations. Ecological Applications, 20:798-815.

Beissinger, S.R., and Westphal, M.I. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management, 62:821–841.

Beissinger, S.R., and McCulloch, D.R. 2002. Population viability analysis. Chicago University Press, Chicago, IL.

Benton, T.G., and Grant, A. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. Trends in Ecology and Evolution, 14:467–471.

Berger, J. 1997. Population constraints associated with the use of black rhinos as an umbrella species for desert herbivores. Conservation Biology, 11:69-78.

Berven, K.A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). Ecology, 71:1599-1608.

Biek, R., Funk, W.C., Maxell, B.A., and Mills, L.S. 2002. What is missing in amphibian decline research: insights from ecological sensitivity analysis. Conservation Biology, 16:728-734.

Blaustein, A.R., Walls, S.C., Bancroft, B.A., Lawler, J.J., Searle, C.L., and Gervasi, S.S. 2010. Direct and indirect effects of climate change on amphibian populations. Diversity, 2:281-313.

Branton, M., and Richardson, J.S. 2011. Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. Conservation Biology, 25:9-20.

Caro, T.M., and O'Doherty, G. 1999. On the use of surrogate species in conservation biology. Conservation Biology, 13:805-814.

Caro, T. 2010. Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species. Island Press.

Carroll, C., Noss, R.F., and Paquet, P.C. 2001. Carnivores as focal species for conservation planning in the rocky mountain region. Ecological Applications, 11:961–980.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology, 215-244.

Davic, R.D. 1984. An investigation of salamander guild predation in a North Carolina stream: An experimental approach. PhD thesis.

Denoël, M., and Ficetola, G.F. 2008. Conservation of newt guilds in an agricultural landscape of Belgium: the importance of aquatic and terrestrial habitats. Aquatic Conservation: Marine and Freshwater Ecosystems, 18:714–728.

Duellman, W.E., and Trueb, L. 1994. Biology of amphibians. JHU press.

Eisenberg, J.F. 1980. The density and biomass of tropical mammals. Pp. 35-55 in M.E. Soulé and B.A. Wilcox (eds), Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachusetts.

Fauth, J.E., 1999. Identifying potential keystone species from field data–an example from temporary ponds. Ecology Letters, 2:36-43.

Fleishman, E., Blair, R.B., and Murphy, D.D. 2001. Empirical validation of a method for umbrella species selection. Ecological Applications, 11:1489-1501.

Fleury, S.A., Mock, P.J., and O'Leary, J.F. 1998. Is the California gnatcatcher a good umbrella species? Western Birds, 29:453-467.

Frankel, O.H., and Soulé, M.E. 1981. Conservation and evolution. Cambridge University Press, Cambridge, United Kingdom.

Fretwell, S.D. 1972. Populations in a seasonal environment (Vol. 5). Princeton University Press.

Frost, C. 2007. History and future of the longleaf pine ecosystem. pp. 9-48 In The longleaf pine ecosystem. Springer, New York, NY.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., and Rubin, D.B. 2013. Bayesian data analysis. CRC press.

Getz, W.M., Marshall, C.R., Carlson, C.J., Giuggioli, L., Ryan, S.J., Romañach, S.S., Boettiger, C., Chamberlain, S.D., Larsen, L., D'Odorico, P., and O'Sullivan, D. 2018. Making ecological models adequate. Ecology letters, 21:153-166.

Goodman, D. 1987. The demography of chance extinction. Pp. 34 in Soulé, M.E. (eds), Viable populations for conservation. Cambridge University Press.

Green, D.M. 2003. The ecology of extinction: population fluctuation and decline in amphibians. Biological Conservation, 111:331-343.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist, 111:1169-1194.

Hanski, I., Moilanen, A., and Gyllenberg, M. 1996. Minimum viable metapopulation size. The American Naturalist, 147:527-541.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, UK.

Harper, E.B., Rittenhouse, T.A., and Semlitsch, R.D. 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.

Hatfield, J.S., Price, A.H., Diamond, D.D., and True, C.D. 2004. Houston Toad (*Bufo houstonensis*) in Bastrop County, Texas. pp.292-298 in Akcakaya H.R. (eds), Species Conservation and Management: Case Studies. Oxford University Press, Oxford, UK.

Heppell, S.S., Caswell, H., and Crowder, L.B. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology, 81:654–665.

Hoctor, T.S., Noss, R.F., Harris, L.D., and Whitney, K.A. 2007. Spatial ecology and restoration of the longleaf pine ecosystem. pp. 377-402 In The longleaf pine ecosystem. Springer, New York, NY.

Houlahan, J.E., and Findlay, C.S. 2003. The effects of adjacent land use on wetland amphibian species richness and community composition. Canadian Journal of Fisheries and Aquatic Sciences, 60:1078–1094.

Jaynes, E.T. 2003. Probability theory: The logic of science. Cambridge University Press.

Lambeck, R.J. 1997. Focal species: A multi-species umbrella for nature conservation. Conservation Biology, 11:849-856.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist, 142:911-927.

Launer, A.E., and Murphy, D.D. 1994. Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. Biological Conservation, 69:145-153.

Li, B.V., and Pimm, S.L. 2016. China's endemic vertebrates sheltering under the protective umbrella of the giant panda. Conservation Biology, 30:329-339.

Mace, G.M., and Lande, R. 1991. Assessing extinction threats: toward a re-evaluation of IUCN threatened species categories. Conservation Biology, 5:148–157.

Maiorana, V.C. 1976. Size and environmental predictability for salamanders. Evolution, 599-613.

Middleton, J., and Green, D.M. 2015. Adult age-structure variability in an amphibian in relation to population decline. Herpetologica, 71:190-195.

New, T.R. 1997. Are Lepidoptera an effective “umbrella group” for biodiversity conservation? Journal of Insect Conservation, 1:5-12.

Norris, K.E.N., 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. Journal of Applied Ecology, 41:413-426.

Noss, R.F., LaRoe, E.T., and Scott, J.M. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. Biological Report 28. Washington, DC: USDI National Biological Service.

Ozaki, K., Isono, M., Kawahara, T., Iida, S., Kudo, T., and Fukuyama, K. 2006. A mechanistic approach to evaluation of umbrella species as conservation surrogates. Conservation Biology, 20:1507–1515.

Pechmann, J.H.K, Scott, D.E., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J., and Gibbons, W. 1991. Declining amphibian populations: The problem of separating human impacts from natural populations. Science, 253:892-895.

Pianka, E.R. 1970. On r-and K-selection. The American Naturalist, 104:592-597.

Pillsbury, F.C., and Miller, J.R. 2008. Habitat and landscape characteristics underlying anuran community structure along an urban–rural gradient. Ecological Applications, 18:1107–1118.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenko, J., and Paine, R.T. 1996. Challenges in the quest for keystones. BioScience,46:609-620.

Quesnelle, P.E., Lindsay, K.E., and Fahrig, L. 2015. Relative effects of landscape-scale wetland amount and landscape matrix quality on wetland vertebrates: a meta-analysis. Ecological Applications, 25:812-825.

Reed, J.M., Mills, L.S., Dunning, J.B., Menges, E.S., McKelvey, K.S., Frye, R., Beissinger, S.R., Anstett, M., and Miller, P. 2002. Emerging issues in population viability analysis. Conservation Biology, 16:7–19.

Roberge, J.M., and Angelstam, P.E.R. 2004. Usefulness of the umbrella species concept as a conservation tool. Conservation Biology, 18:76-85.

Roberge, J.M., Mikusinski, G., and Svensson, S. 2008. The white-backed woodpecker: umbrella species for forest conservation planning. Biodiversity and Conservation, 17:2479–2494.

Rondinini, C., and Boitani, L. 2006. Differences in the umbrella effects of African amphibians and mammals based on two estimators of the area of occupancy. Conservation Biology, 20:170-179.

Rubbo, M.J., and Kiesecker, J.M. 2005. Amphibian breeding distribution in an urbanized landscape. Conservation Biology, 19:504–511.

Salice, C.J., Rowe, C.L., Pechmann,J.H., and Hopkins, W.A. 2011. Multiple stressors and complex life cycles: insights from a population-level assessment of breeding site contamination and terrestrial habitat loss in an amphibian. Environmental Toxicology and Chemistry, 30:2874-2882.

Salvidio, S. 2009. Detecting amphibian population cycles: the importance of appropriate statistical analyses. Biological Conservation, 142:455-461.

Schmidt, B.R., Feldmann, R., and Schaub, M. 2005. Demographic processes underlying population growth and decline in *Salamandra salamandra*. Conservation Biology, 19:1149-1156.

Seddon, P.J., and Leech, T. 2008. Conservation short cut, or long and winding road? A critique of umbrella species criteria. Oryx, 42:240–245.

Semlitsch, R.D. 1983. Structure and dynamics of two breeding populations of the eastern tiger salamander, *Ambystoma tigrinum*. Copeia, 608-616.

Semlitsch, R.D. 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. Copeia, 61–69.

Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., and Gibbons, J.W. 1996. Structure and dynamics of an amphibian community. pp.217-248 in Long-term studies of vertebrate communities. Academic Press.

Semlitsch, R.D. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. Conservation Biology, 16:619-629.

Semlitsch, R.D., and Bodie, J.R. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology, 17:1219-1228.

Semlitsch, R.D., Anderson, T.L., Osbourn, M.S., and Ousterhout, B.H. 2014. Structure and dynamics of ringed salamander (*Ambystoma annulatum*) populations in Missouri. Herpetologica, 70:14-22.

Semlitsch, R.D., Walls, S.C., Barichivich, W.J., and O'Donnell, K.M. 2017. Extinction debt as a driver of amphibian declines: an example with imperiled flatwoods salamanders. Journal of Herpetology, 51:12-18.

Sewell, D., and Griffiths, R. 2009. Can a single amphibian species be a good biodiversity indicator? Diversity, 1:102-117.

Shine, R. 2005. Life-history evolution in reptiles. Annual Review of Ecology, Evolution and Systematics, 36:23-46.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biological Conservation, 83:247-257.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., and Waller, R.W. 2004. Status and trends of amphibian declines and extinctions worldwide. Science, 306:1783–1786.

Suter, W., Graf, R.F., and Hess, R. 2002. Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. Conservation Biology, 16:778-788.

Taylor, B.E., Scott, D.E., and Gibbons, J.W. 2006. Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. Conservation Biology, 20:792-801.

Todd, B.D., Blomquist, S.M., Harper, E.B., and Osbourn, M.S. 2014. Effects of timber harvesting on terrestrial survival of pond-breeding amphibians. Forest Ecology and Management, 313:123–131.

Travis, J. 1994. Calibrating our expectations in studying amphibian populations. Herpetologica, 50:104-108.

Van Langevelde, F., Schotman, A., Claassen, F., and Sparenburg, G. 2000. Competing land use in the reserve site selection problem. Landscape Ecology, 15:243-256.

Van Lear, D.H., Carroll, W.D., Kapeluck, P.R., and Johnson, R. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. Forest ecology and Management, 211:150-165.

Veysey, J.S., Mattfeldt, S.D., and Babbitt, K.J. 2011. Comparative influence of isolation, landscape, and wetland characteristics on egg-mass abundance of two pool-breeding amphibian species. Landscape Ecology, 26:661–672.

Vitt, L.J., Caldwell, J.P., Wilbur, H.M., and Smith, D.C. 1990. Amphibians as harbingers of decay. BioScience, 40:418-418.

Vonesh, J.R., and De la Cruz, O. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia, 133:325-333.

Vos, C.C., and Chardon, J.P. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. Journal of Applied Ecology, 35:44–56.

Wake, D.B., and Vredenburg, V.T. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences, 105:11466–11473.

Ware, S., Frost, C., and Doerr, P.D. 1993. Southern mixed hardwood forest: The former longleaf pine forest. pp. 447–493 In H. Martin, S.G. Boyce, and A.C. Echternacht (eds), Biodiversity of the southeastern United States: Lowland terrestrial communities. John Wiley & Sons, NY.

Watson, J., Freudenberger, D., and Paull, D. 2001. An assessment of the focal-species approach for conserving birds in variegated landscapes in southeastern Australia. Conservation Biology, 15:1364-1373.

Whiteman, H.H., and Wissinger, S.A. 2005. Amphibian population cycles and long-term data sets. pp. 177–184 In Lannoo, M.L. (eds), Amphibian declines: Conservation status of United States species. California University Press, Berkeley.

Winemiller, K.O. 2005. Life history strategies, population regulation, and implications for fisheries management. Canadian Journal of Fisheries and Aquatic Sciences, 62:872-885.