Amphibian and reptile conservation in a changing environment: Case studies from the southeastern United States

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ABSTRACT

The southeastern United States is a global biodiversity hotspot but has experienced severe declines of natural ecosystems. The southeast is currently facing widespread change, particularly from an increasing human population and climate change, that is likely to impact all remaining natural areas to some degree. In this work, I examine some of the challenges currently facing imperiled species of reptiles and amphibians in this region. The work is focused on two species, the Reticulated Flatwoods Salamander (*Ambystoma bishopi*) and the Eastern Indigo Snake (*Drymarchon couperi*) both of which are listed on the U.S. Endangered Species List. Chapter 1 used Light Detection and Ranging (LiDAR) data to measure wetland bathymetry (basin shape) in flatwoods salamander breeding wetlands. Bathymetry data were used to construct stage–area relationships for each wetland, and a history of water level monitoring data were applied to these relationships to build multi-year time series of flooded area metrics. These metrics were then combined with an assessment of vegetation characteristics to map potentially suitable habitat for flatwoods salamander breeding within each wetland. Chapter 2 focused on flatwoods salamander phenology (the timing of life history events) in response to climate change. I quantified flatwoods salamander movements into and out of breeding wetlands over a 10-year period (2010–2020), identifying temperature and precipitation patterns that were conducive to salamander movements. I then used future climate projections to forecast movement

opportunities for flatwoods salamander from 2030–2099 and used an existing hydrologic model built on the same climate data to understand how phenology may interact with hydrology. Overall, only a small number of years are likely to have an ideal intersection of phenology and hydrology as has been observed during recent breeding seasons. Chapter 3 described the construction of a stochastic Integral Projection Model for flatwoods salamanders. I integrated the projections from Chapter 2 with the population model to estimate the viability of two flatwoods salamander populations from 2030–2099 under multiple climate change scenarios. The results indicated that approximately half of the examined scenarios resulted in a high probability (>0.5) of extinction when considering both wetland hydrology and salamander phenology. In Chapter 4, I described the creation of a stochastic Integral Projection Model for indigo snakes. I then demonstrated the utility of this model by examining the effects of initial population size, road density, and removal of individuals to support a captive colony on indigo snake populations. I found that high road densities and high collection rates would likely lead to population declines, although the rate of declines and extinction risk varied across scenarios. Taken together, these projects highlight some of the challenges currently facing herpetofauna in the southeastern United States, demonstrate the difficulty in conserving these often-overlooked species, and provide useful tools for ongoing conservation efforts focusing on these two imperiled species.

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GENERAL AUDIENCE ABSTRACT

We are in the midst of a global biodiversity crisis, with rates of species extinction far exceeding normal levels. Species loss is largely driven by global change attributable to human activities. A rapidly changing world can make it challenging to effectively conserve and manage imperiled species. In this work, I studied two species found only in the southeastern United States that are listed on the U.S. Endangered Species List. Chapters 1–3 focused on the Reticulated Flatwoods Salamander (*Ambystoma bishopi*), while Chapter 4 focused on the Eastern Indigo Snake (*Drymarchon couperi*). In Chapter 1, I used high resolution elevation data to map the shape of flatwoods salamander breeding wetlands. These data were then used to estimate flooded areas across multiple years. Flooded area metrics were combined with vegetation measurements to map potential flatwoods salamander breeding habitat. In Chapter 2, I examined how flatwoods salamander movements may respond to climate change. I identified time periods and weather conditions that coincided with flatwoods salamander movements into and out of breeding wetlands. I then projected potential movement opportunities based on multiple future climate scenarios for each breeding season from 2030–2099. My results showed that few years are likely to be ideal for flatwoods salamander reproduction, which is similar to trends observed in recent years. In Chapter 3, I built a population model for flatwoods salamanders. I then combined the model with predictions made in Chapter 2 to estimate the probability that populations would go extinct by the end of the century. The results indicated that the two flatwoods salamander populations examined had a high probability (>0.5) of extinction in about 50% of the climate scenarios. In Chapter 4, I constructed a population model for indigo snakes using a variety of available data. I used this model to examine the effects of road density, initial population size, and removal of individuals to support a captive colony on indigo snake populations. The results suggested that populations experiencing high road densities or high collection rates were likely to decline over time. These projects highlight some of the difficulties in conserving often-overlooked reptiles and amphibians in the southeastern United States and provide important tools for ongoing conservation projects working with these two imperiled species.

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ATTRIBUTION

This dissertation is comprised of four chapters that were each written as stand-alone publications. Contributions by others rose to the level of co-authorship for all four chapters. Their contributions are briefly described here. Some information among chapters may appear redundant because each chapter is written as a separate manuscript.

Chapter 1. Informing ephemeral wetland conservation using hydrologic regime and LiDAR-based habitat assessments. Daniel L. McLaughlin (Virginia Tech) and Carola A. Haas (Virginia Tech) assisted with conceptualization, study design, and edited drafts of the manuscript.

Chapter 2. Wetland hydrology, not altered phenology, challenges Reticulated Flatwoods Salamander (*Ambystoma bishopi*) management under future climate change. Nicholas M. Caruso (Virginia Tech), George C. Brooks (Virginia Tech), and Carola A. Haas (Virginia Tech) assisted with conceptualization, study design, and edited drafts of the manuscript.

Chapter 3. Predicting the long-term population viability for an imperiled salamander under future climate change. George C. Brooks (Virginia Tech) assisted with conceptualization, study design, and model building. Yan Jiao (Virginia Tech) assisted with model design and implementation. Carola A. Haas (Virginia Tech) assisted with conceptualization and edited manuscript drafts.

Chapter 4. An integral projection model for the imperiled Eastern Indigo Snake (*Drymarchon couperi*). Javan M. Bauder (Arizona Cooperative Fish and Wildlife Research Unit) and Christopher L. Jenkins (The Orianne Society) assisted with conceptualization and study design.

To Aria,
who has brought so much joy to our lives

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PREFACE

The natural world is currently in the midst of a biodiversity crisis, with rates of species imperilment and extinction at least an order of magnitude higher than the typical background rates (Pimm et al. 2014; Ceballos et al. 2015). There are many factors contributing to a loss of biodiversity, but most, if not all, are either directly caused or exacerbated by anthropogenic activities. Habitat loss, fragmentation, and degradation are generally considered the main threats to biodiversity, but there are a myriad of other factors currently contributing to biodiversity loss, including climate change, wildlife disease, pollution, over exploitation, and the introduction of exotic species (Wilson 1989; Tilman et al. 2017). Synergies between these various factors can also exist, potentially exacerbating population declines or leading to unforeseen consequences (Brook et al. 2008). Considering these significant challenges, conservation and management actions must be based on the best available science, contemplate the ecology of the species in question, and account for environmental heterogeneity (both spatial and temporal) to have the highest chance of success.

The extinction of species is preceded by the extirpation of populations. Population loss is currently occurring in both rare and common species at rates that far exceed the rate of elevated species extinctions (Ceballos et al. 2017). The extirpation of populations has broad and important consequences for overall ecosystem structure, function, and services provided to adjacent human populations (Hughes et al. 1997; Gaston and Fuller 2007). For example, the loss of predator populations can have wide ranging effects that cascade through an entire ecosystem, resulting in a different base state (Beschta and Ripple 2009). The extirpation of populations is not restricted to geographic areas experiencing direct habitat loss, with declines occurring even within protected landscapes (Hallmann et al. 2017). Thus, preventing the loss of populations or restoring populations that have already been lost are fundamental challenges in conservation biology.

The longleaf pine (*Pinus palustris*) ecosystem was once dominant across most of the southeastern United States, stretching from southern Virginia to the Florida peninsula and west into eastern Texas. Historically covering over 35 million hectares, longleaf pine forests were reduced to less than 1.3 million hectares by the mid-1990s (Frost 1993). Furthermore, there was, and continues to be, extreme variation in the structure, quality, and functionality of remaining longleaf pine stands. Longleaf pine forests are fire-adapted ecosystems that would have historically experienced regular growing season fires, generally every 1–3 years (Glitzenstein et al. 2003; Stambaugh et al. 2011). These fires reduce leaf litter build-up on the forest floor, promote diversity in the understory plant community (a critical component of these ecosystems), and limit the development of a woody shrub layer (Brockway and Lewis 1997). However, a long history of fire suppression and exclusion has degraded many forest patches in the southeast, regardless of the age or size of overstory pines (Southard 2011). Prescribed fires have returned this regulating mechanism to many well-managed longleaf pine forests, which are characterized by a low density overstory of pines and an understory of thick herbaceous vegetation (Figure 1).

The dramatic decline of the longleaf pine ecosystem has occurred throughout one of the most biodiverse regions in the world, which has been recognized as a global biodiversity hotspot (Noss et al. 2015). The southeastern U.S. supports highly diverse amphibian, reptile, fish, aquatic invertebrate, and plant communities. However, many of the species that inhabit longleaf pine forests have declined significantly, and several species are now listed on the U.S. Endangered Species List. There are numerous challenges for successful conservation of these listed species, including an expanding human population, continued poor fire management of many properties, degraded conditions after decades of logging or agricultural use, and climate change.

This work focuses on two species that exemplify the challenges of reptile and amphibian conservation in the southeastern U.S., building on two long-term research and conservation projects. Flatwoods salamanders are small ambystomatid salamanders that are endemic to the southeastern Coastal Plain. Both sister species, the Reticulated Flatwoods Salamander (*Ambystoma bishopi*) and the Frosted Flatwoods Salamander (*A. cingulatum*) (Pauly et al. 2007), have experienced severe population declines and range contractions, leading them to be listed as Endangered and Threatened under the U.S. Endangered Species Act (O'Donnell et al. 2017). Remaining populations are mostly restricted to large tracts of public land that contain well-managed habitats (e.g., military bases, national forests, and national wildlife refuges). Even though remaining populations are generally protected from direct habitat loss and occur in well-managed landscapes, issues impacting the habitat quality of uplands, connectivity of uplands and wetlands, the habitat quality in breeding wetlands (e.g., application of prescribed fire during the winter months), and the success of breeding events persist (Means et al. 1996; Bishop and Haas 2005; Palis et al. 2006). These issues have led to additional extirpation of populations even after listing and management actions were implemented.

Flatwoods salamanders inhabit mesic pine flatwoods (low-lying longleaf pine forests; Figure 1) and have a life cycle consisting of a terrestrial egg phase, an aquatic larval phase, and a terrestrial adult phase (Figure 2). Adults migrate seasonally to breeding wetlands in the fall or early winter (Palis 1997; Erwin et al. 2016), and female salamanders deposit eggs in dry wetland basins (Anderson and Williamson 1976). Eggs begin development terrestrially and hatch after they are inundated as wetlands fill from seasonal rains. Larval salamanders remain in the wetland for 11–18 weeks before undergoing metamorphosis and emigrating back into the surrounding uplands (Palis 1995). This relatively long larval period makes flatwoods salamanders susceptible to complete reproductive failure during drought years and years in which wetlands are flooded intermittently (Palis et al. 2006).

The Reticulated Flatwoods Salamander portion of this work is a continuation of a long-term conservation and research project occurring on Eglin Air Force Base in the Florida Panhandle, which represents one of the last remaining strongholds for this species. In Chapter 1, I expand on previously conducted studies examining flatwoods salamander breeding wetland hydrology (e.g., Chandler et al. 2017) by using Light Detection and Ranging (LiDAR) data to characterize wetland bathymetry or basin shape. I then combine bathymetric maps with a history of water level monitoring in the same wetlands to build a multi-year time series of flooded area metrics. Finally, I also use LiDAR data to quantify vegetation structure within the same set of wetlands, ultimately creating predictions about flatwoods salamander habitat that consider both hydrologic and vegetative characteristics within each breeding wetland.

Chapters 2 and 3 are part of a large, multi-partner project examining the effects of climate change on salamander phenology (i.e., the timing of life history events). In Chapter 2, I assess climate factors that initiate flatwoods salamander movements into and out of breeding wetlands. I then evaluate the potential for salamander movements during each breeding season from 2030–2099 using a suite of climate models and emission scenarios. In each year, phenology predictions are integrated with an existing hydrologic model (built using the same climate data; Chandler et al. *In prep*) to assess whether phenological mismatch is likely to impact the management of flatwoods salamander populations in the coming decades. In Chapter 3, I expand on an Integral Projection Model (IPM), initially developed by Brooks (2020), to assess the effects of climate change on long-term flatwoods salamander population viability. I use this model to better understand flatwoods salamander demography, including identifying critical knowledge gaps, and to estimate extinction probability under different climate scenarios. Future projections rely on the work completed in Chapter 2 and that of Chandler et al. (*In prep*) to estimate the quality of future breeding seasons (see flowchart in Appendix B: Figure S1 for an overview of the process detailed in Chapters 2 and 3). Overall, the results of Chapters 1–3 are used to make conservation and management recommendations for this imperiled amphibian.

The last chapter of this dissertation focuses on the Eastern Indigo Snake (*Drymarchon couperi*). Indigo snakes are the longest snake native to North America, with males occasionally reaching lengths exceeding 2.4 meters (Figure 3). Historically, indigo snakes were native to parts of southern Mississippi, Alabama, Georgia, and all of Florida. Today, populations have been extirpated from the western portion of their historic range and occur only in southern Georgia and peninsular Florida (Figure 4). Range contractions and evidence of population declines in other regions led the U.S. Fish and Wildlife Service to list indigo snakes as Threatened on the Endangered Species List in 1978 (USFWS 1978). This listing status has largely removed some potential threats to indigo snake populations (e.g., collection for the pet trade) but other serious threats remain (habitat loss, fragmentation, and disease), resulting in continued listing of the species after the most recent status assessment (USFWS 2019).

Indigo snakes are highly mobile (sometimes moving over two kilometers in a single day) and possess one of the largest known average home range sizes (500–1,000 ha) of any snake species (Breininger et al. 2011; Hyslop et al. 2014; Bauder et al. 2016). While typically described as an upland species, indigo snakes spend a significant amount of time foraging along wetland edges where food resources are plentiful (Hyslop et al. 2014; Bauder 2018). In the norther portion of their range, indigo snakes are tightly linked to the presence of Gopher Tortoises (*Gopherus polyphemus*) because tortoise burrows provide refugia from otherwise lethal winter temperatures (Stevenson et al. 2003; Hyslop et al. 2009).

Despite the current conservation concern for this species, there have been no broad assessments of population viability (but see Folt et al. [2019] and Bauder [2019] for site-specific examples). In Chapter 4, I integrate a variety of existing datasets from wild indigo snake populations and the captive breeding colony to construct a population model for representative indigo snake populations. I demonstrate the utility of this model for guiding often complex decisions within ongoing indigo snake conservation projects by examining the effects of initial population size, road density, and collection to support the captive colony on indigo snake populations. Similar to the above work, the results of Chapter 4 are then used to make conservation and management recommendations for this imperiled but charismatic species.

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Figure 1. The characteristic vegetation structure of a well-managed longleaf pine forest (top), and a pine flatwoods wetland embedded within the surrounding upland pine forest (bottom). Photo credit: Houston Chandler.

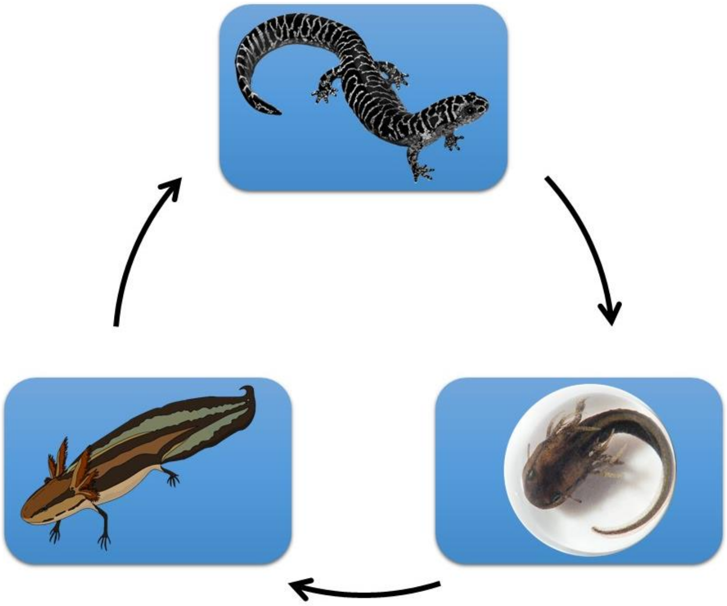

Figure 2. The life cycle of flatwoods salamanders consists of a terrestrial adult phase, a terrestrial egg that hatches once inundated by water, and an aquatic larval stage. Images provided by P. Hill (egg), E. Browning (larva), and M. Mandica (adult).

Figure 3. An Eastern Indigo Snake (*Drymarchon couperi*) from southeastern Georgia. Photo credit: Houston Chandler.

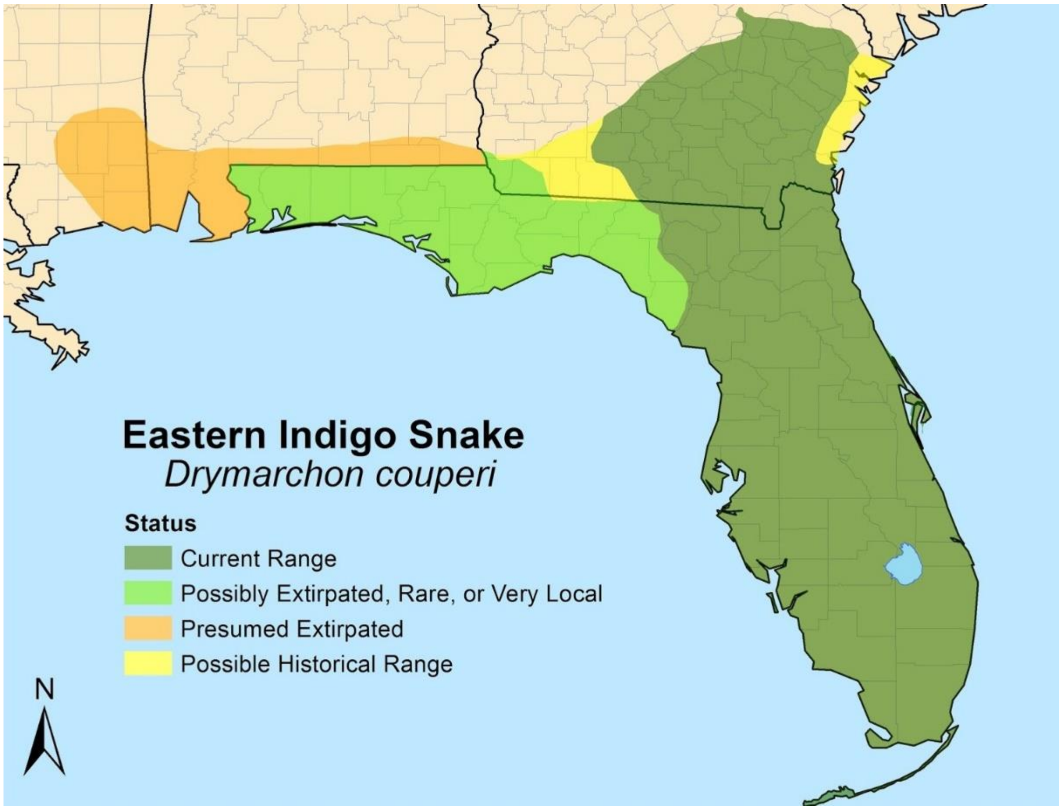

Figure 4. The approximate current and historic distribution of the Eastern Indigo Snake (*Drymarchon couperi*).

CHAPTER 1

Informing ephemeral wetland conservation using hydrologic regime and LiDAR-based habitat assessments

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Abstract

Integrated assessments of wetland hydrologic regime and other environmental factors are key to understanding the ecology of species breeding in ephemeral wetlands, and reproductive success is often directly linked to suitable flooding regimes, both temporally and spatially. We used high-resolution Light Detection and Ranging (LiDAR) data to develop stage–flooded area relationships, predict spatial extent of flooding, and assess vegetation structure in 30 pine flatwoods wetlands. We then integrated bathymetric data with existing water level data in a subset of wetlands to create multi-year time series of daily flooded areas and related observed flooded areas to landscape topographic metrics to develop models predicting flooded extents at wetlands without monitoring wells. We found that stage–area relationships varied across wetlands and indicated that a one cm increase in water depth could generate flooded area increases ranging from hundreds to thousands of square meters, depending on wetland size and bathymetry. Flooded areas frequently fragmented into numerous discrete flooded patches as wetlands dried, and there was only a weak positive correlation between hydroperiod and mean flooded area (r = 0.32). To demonstrate the utility of using LiDAR data to assess wetland bathymetry when considering the ecology and conservation of wetland-breeding species, we combined metrics of flooding and vegetation to map potentially suitable habitat for the imperiled Reticulated Flatwoods Salamander (*Ambystoma bishopi*). Overall, projects focusing on wetland-breeding species would benefit from coupled assessments of bathymetry, water level dynamics, and other wetland characteristics to identify specific effects of within-wetland habitat variation on species ecology and fitness.

Introduction

Globally, widespread loss and degradation of wetland ecosystems have occurred through a variety of anthropogenic mechanisms, reducing wetland area and eroding the functionality of remaining wetlands (Davidson 2014; Allen et al. 2020). This is especially true for ephemeral, often geographically isolated wetlands (i.e., lacking a consistent surface water connection; Tiner 2003) that occur within many low-relief landscapes (e.g., the southeastern Coastal Plain and Prairie Pothole regions of the United States; Lane and D'Amico 2016). Yet, such systems provide critical habitat for a variety of wildlife species (Jenkins et al. 2001; Gibbons et al. 2006; Skagen et al. 2008) and contribute to landscape-scale hydrologic processes, nutrient cycling, and connectivity (McLaughlin et al. 2014; Uden et al. 2014; Capps et al. 2015; Cohen et al. 2016; Smith et al. 2018).

Many ephemeral wetlands are highly productive systems that support diverse species assemblages during periods of temporary flooding (Wilbur 1980; Dodd and Cade 1998; Tarr et al. 2005; Gibbons et al. 2006; Martin and Kirkman 2009; Lukács et al. 2013). This includes fully aquatic, semi-aquatic, and terrestrial species that can forage in and around shallow wetlands (Kantrud and Stewart 1977; Russell et al. 2002; Eskew et al. 2009; Daniel et al. 2021). For aquatic species or life stages, exploiting these productive environments presents a tradeoff of limited predation pressure at the risk of desiccation from drying before reaching a size or development stage suitable for metamorphosis to a terrestrial adult or a desiccation-resistant stage (Williams 1985; Semlitsch 1987; Wellborn et al. 1996; Skelly 1997). Importantly, the environmental conditions experienced by aquatic larvae are intrinsically linked to adult life after metamorphosis, and carry-over effects can impact multiple aspects of adult ecology (James and Semlitsch 2001; Yagi and Green 2018). Effectively quantifying the environmental conditions experienced by aquatic larvae in temporary environments and connecting them to the ecology of the adult population may provide a better understanding of fundamental ecological processes (Earl and Semlitsch 2013; Brooks et al. 2020).

For amphibians with long development times, the hydrology of ephemeral breeding wetlands and its interaction with other aspects of the wetland environment, particularly vegetation structure, are key factors determining reproductive success (Semlitsch 2000). Hydroperiod (the duration of inundation) defines the ultimate bounds of the larval period and has thus been most frequently used to characterize the hydrologic conditions within a wetland during amphibian breeding seasons (e.g., Pechmann et al. 1989; Snodgrass et al. 2000) or used in manipulative experiments examining larval amphibian ecology (e.g., Wilbur 1987; Amburgey et al. 2016). Longer hydroperiods can increase overall amphibian productivity (Wilbur 1987; Semlitsch et al. 1996) and size at metamorphosis (Brooks et al. 2020). However, as a metric, hydroperiod represents a limited characterization, both temporally and spatially, of the hydrologic conditions within a wetland, especially when considered as a binary distinction between wet vs. dry (Bischof et al. 2013). Spatiotemporal variability in habitat quality within a wetland is ultimately controlled by multiple aspects of the hydrologic regime, including hydroperiod, the timing and rate of filling and drying events (Church 2008; Chandler et al. 2017), the spatial configuration of flooded areas (McLean et al. 2021), and how these factors relate to other environmental characteristics. To date, few studies (but see Brice et al. 2022) have attempted to integrate a complete characterization of within wetland spatiotemporal variation in flooding regimes with amphibian conservation.

Bathymetry (wetland basin shape) determines the spatial configuration and depth of inundation within a wetland, ultimately controlling what habitat is inundated in wetlands with a heterogeneous distribution of habitat types (Haag et al. 2005). For example, as water levels rise, multiple small, flooded depressions may combine into larger wetted areas, significantly altering the amount of flooded habitat available to aquatic species (Wu and Lane 2016, 2017). Furthermore, spatial variation in flooded area could coincide with spatial heterogeneity in vegetation characteristics or directly influence wetland vegetation, impacting the quality of habitat in the aquatic environment (Malhotra et al. 2016; McLean et al. 2021). On-the-ground measurements of wetland bathymetry and thus flooded area assessments are resource intensive, limiting application across many wetland systems. Yet, high-resolution topographic data are increasingly available via Light Detection and Ranging (LiDAR) and can be used to create stage–area relationships that describe flooded areas based on water depth (Jones et al. 2018a). For wetlands where water level data are readily available, these relationships become a useful tool to better understand the spatiotemporal variability of flooded areas and thus to inform conservation efforts in monitored systems. Another advantage of LiDAR data is that it can be used to map vegetation within wetlands (Luo et al. 2014), allowing researchers to assess multiple components of wetland habitat using a single data source.

Water level monitoring is a resource-intensive effort and informing larger scale conservation efforts requires predictions of flooding dynamics across the distribution of wetlands within a landscape. High-resolution topography data provide one important element of wetland hydrology (bathymetry) but may also inform flooded depth and area predictions (Haag et al. 2005; Jones et al. 2018a). Ephemeral wetland hydrology is characterized by strong responses to regional climate forcing (i.e., precipitation and evapotranspiration; Riekerk and Korhnak 2000; Brooks 2004; Park et al. 2014). However, groundwater fluxes (inflows or outflows) can also be dominant and variable across systems (Winter and LaBaugh 2003) via landscape topographic characteristics (Winter 1988; Cianciolo et al. 2021). As such, relationships between observed water level regimes and landscape topographic metrics may offer an additional use of available LiDAR data to predict inundation characteristics in other similarly situated wetlands, informing landscape-scale assessments.

We used high-resolution LiDAR data to measure wetland bathymetry, vegetation structure, and surrounding landscape characteristics of ephemeral wetlands embedded within pine flatwoods of the southeastern United States Coastal Plain. We demonstrate the utility of these techniques for broadly understanding spatiotemporal variability in water levels within ephemeral wetlands and for specific conservation applications, using habitat delineations for the imperiled reticulated flatwoods salamander (*Ambystoma bishopi*) as a case study.

Methods

Study System

We studied depressional wetlands embedded within pine flatwoods located on Eglin Air Force Base in Okaloosa and Santa Rosa counties, Florida. The study area is characterized by poorly drained, sandy soils with high water tables, creating numerous ephemeral wetlands across the landscape (see supplementary material for additional details). Wetlands typically contain a pine overstory and an understory of thick herbaceous vegetation, but some wetlands have developed a woody midstory in the absence of regular wildfires. Legacy effects of fire exclusion combined with current logistical challenges of prescribed fire application and ongoing mechanical and herbicide treatments have created a variety of wetland vegetation characteristics within the study area (Varner et al. 2005; Gorman et al. 2013; Appendix A: Figure S1).

Pine flatwoods wetlands provide critical breeding habitat for flatwoods salamanders (O’Donnell et al. 2017). Adult salamanders (Appendix A: Figure S2) migrate to breeding wetlands seasonally where they deposit eggs in dry wetland basins (Anderson and Williamson 1976). The presence of herbaceous vegetation in and around breeding wetlands plays a critical role at multiple stages of the flatwoods salamander life cycle, including as egg deposition sites (Gorman et al. 2014), habitat for larval salamanders and their prey (Sekerak et al. 1996; Gorman et al. 2009; Chandler 2015), and potentially as foraging sites or refugia for juvenile and adult salamanders (Jones et al. 2012). In addition to needing suitable vegetation, successful recruitment depends on suitable hydrology that inundates terrestrial eggs, supports an 11–18-week larval period, and has a recession rate conducive to metamorphosis (Palis 1995; Chandler et al. 2017). Thus, high-quality breeding habitat for flatwoods salamanders depends on the intersection of appropriate vegetation and flooding regimes that allow salamanders to complete their development period.

LiDAR Data Processing

We used LiDAR data provided by Jackson Guard (Eglin’s Natural Resources Division). The data were collected on 17 April 2018 with a Leica ALS80 airborne LiDAR sensor and were determined to have a root mean square error of 0.049 m (vertical accuracy) using ground control points. Data provided were pre-processed into a Digital Elevation Model (DEM, representing the ground surface) and Digital Surface Model (DSM, representing the tallest surface [e.g., vegetation]), both of which had a pixel resolution of 0.501 x 0.501 m. Prior to analyses, we filled all single cell pits in the raster layers using the Whitebox Package (Wu 2020) and smoothed the DEM and DSM by calculating mean cell values within a 3 x 3 moving window (Jones et al., 2018a). The datasets covered an area that included 30 pine flatwoods wetlands, and we conducted all analyses based on wetland boundaries that were delineated in the field using a combination of high-water levels and wetland-specific vegetation.

Hydrologic Metrics

Of the 30 wetlands included in our analyses, 14 had water level monitoring wells installed at the time of LiDAR data collection. We installed monitoring wells at the approximate deepest point of the wetland (installation dates ranged from 17 August 2012 to 17 November 2017) and placed a HOBO® U20 pressure transducer (Onset Computer Corporation, Bourne, MA) within each well. We converted 15-minute pressure measurements to water levels (relative to ground surface), correcting for barometric pressure variation using a U20 logger placed in the well head space. We calculated daily water levels as the mean water level from 23:00–1:00 and used these values for all analyses.

We used the processed DEM to calculate stage–area relationships based on wetland bathymetries for all wetlands in the study area using the general methodologies of Jones et al. (2015, 2018a). Beginning at the minimum elevation in each wetland, we incrementally filled each wetland basin by 0.01 m. For each 0.01 increase in water level, we calculated the flooded area in the wetland basin based on the number of pixels that would be inundated at that water level. These calculations created stage–area curves for each wetland beginning at the lowest elevation and increasing to a water depth that completely flooded the delineated basin.

We then refined stage–area relationships based on whether or not wetlands were partially inundated when the LiDAR data were collected. Topographic LiDAR sensors do not penetrate water and cannot be used to measure wetland bathymetry in flooded portions of a wetland

(Quadros et al. 2008). We determined that 12 of 14 wetlands with available water level data were partially flooded when the LiDAR data were collected. For the two dry wetlands, we made no changes to the stage–area curves generated from the bathymetry data. In the 12 wetlands known to be partially flooded, we accounted for this uncertainty when measuring wetland bathymetries by defining all elevations within 0.1 m of the minimum within-wetland DEM elevation (twice the vertical accuracy of the LiDAR data to capture error in both directions) as the probable flooded area at the time of data collection. We then shifted the stage–area curves so that 0.1 m above the lowest elevation (i.e., the extent of the hypothesized flooded area) now represented the water depth recorded on April 17. All values above this elevation we interpreted as correctly defined by sequentially inundating the dry areas of the wetland basin using the DEM. To estimate the underwater portion of the stage–area curve, we modified previously published equations that relate wetland stage to flooded area (Hayashi and van der Kamp 2000; Minke et al. 2010). This relationship is a power function given by the equation:

$$A = s * (\frac{z}{h_0})^p \tag{1}$$

where A is the predicted flooded area, s is the flooded area on April 17, z is the wetland stage (i.e., water depth), h_0 is the wetland stage on April 17, and p is a constant that defines the shape of the stage–area curve. We estimated p for each wetland using nonlinear least squares estimation and a dataset that included the origin and the first four stage–area values calculated from the LiDAR data because these values maintained a relatively constant slope that was most closely related to the portion of the stage–area curve being estimated. Thus, the final stage–area curve for the 12 wetlands known to be partially flooded had an estimated underwater portion derived from Equation 1 and an above water portion estimated from the bathymetry of dry areas within the wetland basin.

In the 16 wetlands with no available water level data, we assumed that all wetlands were partially flooded when the LiDAR data were collected. We again defined all elevation values within 0.1 m of the minimum DEM elevation within that wetland as the probable flooded area. For these wetlands, we simply removed portions of the stage–area curves below 0.1 m because no further correction could be made.

To better understand flooding dynamics within wetlands, we used the bathymetry data from all wetlands (n = 30) to examine the spatial distribution of flooded patches as wetlands filled. We calculated the number of discrete (i.e., not connected) flooded patches in each wetland at elevations ranging from 0.1–0.5 m above the lowest elevation in 0.05 m increments (i.e., this did not include portions of wetlands predicted to be flooded). We also calculated the area of the largest patch relative to the total flooded area of all patches. For these calculations, we only considered flooded patches that were at least 1 m^2.

To more specifically assess flooding dynamics within the flatwoods salamander breeding season, we used the derived stage–area curves and all existing well data to estimate daily flooded areas for each day with a water level measurement in the 14 wetlands with well data. In these wetlands, we examined the correlation between hydroperiod and mean flooded area across four flatwoods salamander breeding seasons (November–May, 2015–2019). We focus our analyses on these four breeding seasons because they maximize the overlap in available monitoring well data and had characteristics that offered the potential for successful flatwoods salamander reproduction in some wetlands (Haas, unpublished data). We calculated hydroperiod as the longest period of continual surface water that at least partially overlapped the breeding season.

Mean flooded area was calculated by including only days with at least some water in the wetland and was standardized by the total area of each wetland basin.

To examine the spatial extent of flooding in the 14 wetlands with well data, we calculated the percentage of days that each pixel would have been inundated when there was some water in the wetland during the 2015–2019 breeding seasons. For this analysis, we had no way to spatially differentiate water depths within areas predicted to be flooded during the LiDAR data collection. Therefore, we assessed flooding variation based only on water depths greater than those recorded on 17 April 2018. We assigned all pixels predicted to be flooded during LiDAR collection a 100% chance of being flooded at these water depths. For the two dry wetlands, we only considered water depths greater than 5 cm. Thus, this metric of flooding is relative to wetlands being partially flooded.

Landscape Topographic Metrics

To examine the effect of landscape factors on flooded area in wetlands, we used the DEM to calculate 10 landscape metrics following Cianciolo et al. (2021). These metrics were calculated using tools in the Whitebox package (Wu 2020) and generally described various aspects of the terrain and landscape position (Appendix A: Table S1). For all metrics, we smoothed the resulting raster layer by calculating the mean value in a 5 x 5 moving window surrounding each pixel. We summarized values for each wetland by calculating the mean value within the delineated wetland basin. We also included the mean elevation within each wetland, the mean difference in elevation between pixels within the wetland and adjacent upland pixels occurring within a 50 m buffer, and the wetland area in the following analysis. This resulted in 13 metrics describing each wetland's size and landscape position (deviation from mean elevation, slope, topographic wetness index, ruggedness index, contributing area, downslope distance, downslope index, plan curvature, profile curvature, height above nearest drainage, mean elevation within each wetland, difference in elevation, and wetland area).

Prior to analyses, we centered and scaled all metrics by subtracting the mean and dividing by the standard deviation. We also dropped five metrics from the dataset (ruggedness index, slope, downslope distance, deviation from mean elevation, and profile curve) because they were correlated with other metrics ($|r| \geq 0.65$; Appendix A: Table S2). We fit linear regression models using the remaining eight metrics to predict the median flooded area across four flatwoods salamander breeding seasons (2015–2019) in the 14 wetlands with monitoring well data. We again defined the breeding season as occurring from November–May and calculated a single median flooded area for each wetland using all periods with at least some water in the wetland. We standardized flooded area metrics by wetland area to account for the large difference in wetland sizes across the study area. We fit all subsets regression using the *Leaps* package in R (Lumley and Miller 2020) and restricted the analysis to include a maximum of two landscape metrics per model to reduce the possibility of overfitting the model. We did not include any interaction effects in these models. We selected the best model using a combination of the Bayesian Information Criteria (BIC) and adjusted R^2. We then used the top model to estimate the median flooded area in the 16 wetlands without monitoring well data.

Vegetation Metrics

To estimate vegetation height, we subtracted the DEM from the DSM layer. We then delineated the vegetated areas in each wetland that appeared suitable for flatwoods salamander eggs and larvae. We defined these areas as all pixels with a vegetation height of less than 1.0 m (i.e., areas with vegetation heights indicative of herbaceous vegetation and not shrubs or trees). We made no correction to the vegetation metric for predicted flooded areas in wetlands because depths measured on April 17 were generally not deep enough to misrepresent shrubs as part of the herbaceous layer, and we had no way to spatially delineate water depths within the predicted flooded area.

Potential Flatwoods Salamander Habitat

We combined the results of the hydrologic metrics, landscape topography, and vegetation metrics to predict the location of potentially suitable flatwoods salamander habitat. For sites with well data, we used known stage–area relationships and water level data to map frequently flooded areas as described above. For sites without well data, we used the best performing landscape model to estimate median flooded area. Starting at the lowest elevation, we identified all pixels that would be flooded at the median flooded area, assuming wetlands flooded sequentially from low to high elevations. We were unable to predict spatial flooding patterns in one wetland that had an estimated median flooded area less than the area that we estimated was flooded at the time of LiDAR collection.

We identified all wetland pixels that were characterized by high-quality hydrologic conditions (i.e., either flooded during 50% of available water level measurements or the predicted median flooded area from the top landscape model), high-quality vegetation conditions (i.e., vegetation heights less than 1.0 m), or both. To better understand the utility of these predictions, we identified the percent overlap with on-the-ground delineations of mixed herbaceous habitats believed to be suitable for flatwoods salamanders. Briefly, in 11 wetlands, we mapped mixed herbaceous habitats in 2016 using expert site knowledge and a combination of handheld GPS units and Google Earth (Google, Mountain View, CA, USA). We defined these habitats as areas larger than 1 m^2 that were dominated by herbaceous vegetation known to provide egg-laying habitat for flatwoods salamanders (Gorman et al. 2014). All other analyses were performed in R version 4.1.1 (R Core Team 2020).

Results

Hydrologic Metrics

Across the study area, elevation ranged from 0.96–14.15 m above sea level (asl; mean = 7.55 m asl), and elevations within wetland basins ranged from 6.7–11.1 m asl (mean = 8.9 m asl). Wetlands were characterized by shallow basins, with little elevation gain from the lowest to highest points (mean elevation gradient: 1.1 m; range: 0.33–2.7 m). Higher elevations within wetland basins typically represented hummocks or raised areas along wetland edges that were unlikely to be inundated during normal conditions (Figure 1A). In the 12 wetlands that were known to be partially flooded during LiDAR data collection, water depths ranged from 7.6–32.4 cm, translating to flooded areas of 6.5–42% of the mapped wetland basins (Table 1). In wetlands with no well data, the predicted flooded area during LiDAR data collection ranged from 0.1–40% of the total wetland area (Table 1).

Stage–area relationships were similar across all wetlands, but the magnitude of changes in flooded area with water depth increases depended on the size and shape of the wetland (Figure 2). Wetland areas ranged from approximately 833–96,595 m^2 (Table 1), and stage–area relationships indicated that, depending on the wetland, a 1 cm increase in depth could generate flooded area increases ranging from hundreds to thousands of m^2. As water levels increased within wetlands, many disjointed flooded areas formed before coalescing into a single larger wetted area (Figure 3A). By the time that wetlands reached approximately 50% of their maximum depth, a single large, flooded area tended to dominate the wetland basin (Figure 3B). Furthermore, the stage–area relationships indicated that some wetlands experienced water levels exceeding the inflection point on the curve (i.e., when the entire wetland area is flooded) and thus indicate conditions of overflow from wetland basins into the surrounding flatwoods (Figure 1B).

From 2015–2019, the number of daily flooded area values that were estimated using Equation 1 (see Appendix A: Table S3 for model results) was highly variable across wetlands (ranging from 20.8–89.2% of all values; Appendix A: Table S4). On average, estimated flooded areas accounted for only 1.7–12.8 percent of the maximum flooded area within a wetland (Appendix A: Table S4), highlighting that these values represented the bottom of the stage–area relationship (Figure 2A). Flooded areas across all 14 instrumented wetlands tended to be highest during the flatwoods salamander breeding season (i.e., November–May; Figure 4A) but were highly variable across years and wetlands (Figure 4B). In addition to this temporal variability, there was also considerable variation in the proportion of each wetland that was typically flooded. When water was present in the wetland, some wetlands had flooded areas that were most commonly near their maximum flooded area for that breeding season, while others were typically only partially flooded (e.g., Site 36 in 2015–2016 vs. Site 15 in 2016–2017; Figure 4B). Over these four breeding seasons, hydroperiod was positively, but weakly, correlated to the mean flooded area when standardized by maximum area of each wetland (Pearson’s $r = 0.32$). A hydroperiod increase of 9 days would, on average, coincide with an approximately 10% increase in flooded area.

Landscape Topographic Metrics

Of the eight landscape metrics that we evaluated, wetland area was the best single predictor of median flooded area (when standardized by wetland area) during the flatwoods salamander breeding season (N = 14, adjusted $R^2 = 0.25$, $F_{1,12} = 5.29$, $P = 0.04$; Appendix A: Table S5). Wetlands with smaller total areas tended to have a higher percentage of their basins flooded than larger wetlands (Table 2). The best multiple linear regression model included both wetland area and the mean elevation within a wetland (adjusted $R^2 = 0.49$, $F_{2,11} = 7.2$, $P = 0.01$; Appendix A: Table S5). Again, larger wetlands typically had a lower percentage of their basin flooded than smaller wetlands. Wetlands with basins at higher elevations tended to be more flooded than lower wetlands (Table 2). Using the multiple linear regression model, we predicted median flooded area in 15 wetlands without well data (Table 1).

Vegetation Metrics

Across the study area, vegetation heights in wetlands ranged from near 0 to over 20 m. There was substantial variability in the vegetation structure among wetlands, with some wetlands being dominated by herbaceous vegetation, while others had large amounts of shrubs and trees (Figure 5A). Wetlands with vegetation characteristic of a fire-maintained system contained mostly herbaceous vegetation interspersed with canopy trees and small patches of woody shrubs (Figure 5B). Herbaceous vegetation was frequently mapped near wetland edges.

Potential Flatwoods Salamander Habitat

We used the LiDAR-derived hydrologic and vegetation metrics to delineate areas with potentially suitable flatwoods salamander habitat in 29 wetlands (median flooded area observed for 14 wetlands and predicted for 15 wetlands) (Table 1). Across all sites, there were examples of wetlands that tended to be hydrologically limited and wetlands that were limited by suitable vegetation (Figures 6A and 7). We tested the accuracy of habitat predictions by comparing the results to 19 field-delineated habitat patches in 11 wetlands. There was broad but variable overlap between remotely sensed habitat predictions and field-delineated habitat patches in most wetlands (Figures 6B and 7). Five of the 19 (26.3%) field-delineated patches were characterized by at least 50% of pixels having both high quality vegetation and hydrologic characteristics, while 15 of 19 (78.9%) patches had greater than 50% of their area covered by high-quality vegetation, high-quality hydrologic conditions, or both (Figure 6B). Areas outside of the field-delineated patches often contained potentially suitable habitat according to the LiDAR-derived predictions (Figure 7).

Discussion

Our study used water level observations and wetland bathymetry to characterize the spatiotemporal variation in flooding regimes within ephemeral wetland systems. The effects of variation in flooding regimes within natural systems have been considered for some taxa (e.g., beavers; Hood and Larson 2015), and wildlife managers have long manipulated water depth and extent of flooded area to achieve certain goals for seeding and survival of wetland plants and to attract migratory shorebirds or wintering waterfowl (Rundle and Frederickson 1981; Collazo et al. 2002; Colwell and Taft 2002). However, these principles have rarely been applied in relation to either amphibian ecology or conservation. Instead, the amphibian literature has predominantly focused on hydroperiod when considering the effects of wetland hydrology (Pechmann et al. 1989; Snodgrass et al. 2000; Walls et al. 2013). This is likely driven by several factors, including the ease of measuring hydroperiod relative to other hydrologic metrics, the ability to manipulate hydroperiod in experimental systems, the ultimate constraints imposed on reproduction by hydroperiod, and the detailed spatial data needed to relate many metrics of amphibian breeding success to wetland bathymetry. Yet, we found only a weak positive correlation between flooded area and hydroperiod across four flatwoods salamander breeding seasons, suggesting that flooded area is a complementary metric that describes portions of the hydrologic regime not captured by hydroperiod alone. Thus, despite the advantages of hydroperiod as a metric (it has been useful in many studies including our own work; Pechmann et al. 1989; Semlitsch 2000; Snodgrass et al. 2000; Gibbons et al. 2006; Chandler et al. 2016), we argue that amphibian conservation and our understanding of amphibian ecology would benefit from including a broader understanding of the spatiotemporal variability in wetland hydrologic characteristics and their overlap with other environmental parameters.

We mapped wetland bathymetries using high-resolution LiDAR data, reducing the investment needed to measure bathymetry when compared to field surveys (Wilcox and Huertos 2005). Bathymetry data allowed us to generate stage–area relationships for a suite of wetlands, and we were then able to leverage existing monitoring well data from a subset of wetlands to measure temporal trends in flooding dynamics, expanding the hydrologic metrics that we could generate with the bathymetry data. Furthermore, we used a variety of landscape topographic metrics to make predictions about flooded area in wetlands with no well data. Our results indicated that wetlands in our study area varied in flooding dynamics but that most were characterized by relatively large increases in flooded area as a response to small increases in water depths. This is perhaps not surprising given the minimal topography within wetland basins, but it highlights how fluxes of even small amounts of water may have substantial effects on flooded extents and thus aquatic organisms in these wetlands. For example, vegetation management that either increases (i.e., fire suppression) or decreases (e.g., prescribed fire) evapotranspiration rates may have disproportionate effects on flooding extents (Jones et al. 2018b). It may also be feasible to artificially increase both hydroperiod and flooded area in years when conditions are borderline for amphibian reproduction by pumping water into wetlands (Seigel et al. 2006, Hamer et al. 2016, Mathwin et al. 2020), but this type of active management can be logistically difficult to plan without an understanding of how much water is needed to improve breeding habitat.

At low water levels, the flooded area within most wetlands consisted of a collection of discontinuous patches, which may affect amphibian larval dispersal, growth, and survival. Fragmenting of a single flooded area into multiple patches could elevate larval densities, increasing competition and potentially causing larvae to metamorphose at smaller body sizes (Wilbur 1997; Leips et al. 2000). Furthermore, experimental studies have suggested that habitat patch size can impact survival and growth rate of tadpoles but that these effects are not consistent across species (Pearman 1993, 1995). Habitat patches may also vary in the amount of resources available, especially for habitat specialists like flatwoods salamanders that could be forced into patches of less favorable conditions as wetlands dry (i.e., deeper areas with dense shrub cover and less herbaceous vegetation; Chandler et al. 2017). The size of flooded patches can also impact predation pressure as invertebrate predators tend to colonize larger patches (Pearman 1995), but other predators may reach higher densities in drying wetlands (Herteux et al. 2020). In years where wetland water levels fluctuate between full pool and 10–40% inundated, the effects of variable patch sizes could occur repeatedly over a single breeding season. If individuals occupy multiple patches as wetlands dry, there is a high probability that different portions of a population would experience different hydroperiods and recession rates.

The considerable variation in flooding regimes among instrumented wetlands highlights the need for such information across the full suite of wetlands in a particular landscape. To that end, we developed a model to predict flooded areas using landscape topographic metrics. We found that larger wetlands had a lower percentage of their basins flooded at the median flooded area. These wetlands take much higher volumes of water to fill and may also experience disproportionate effects of increased evapotranspiration because of fire suppression (Jones et al. 2018b). The two-factor model that we used to make predictions also contained a positive effect of mean wetland elevation. This effect is more challenging to interpret but is likely attributable to differences in basin shape (i.e., cylindrical vs. conical wetlands) and the presence of inundated pixels in the elevation calculation (i.e., higher than the true elevation). Indeed, several of the landscape metrics used in our analysis have uncertainty added because of flooded areas at the time of LiDAR data collection. Furthermore, if LiDAR data had been collected when wetlands were dry, allowing for a complete description of the stage–area curve in all wetlands, then parameters describing a wetland’s shape could be incorporated into this type of analysis. Despite these limitations, our application required the best predictive model to make predictions about potentially suitable salamander habitat over a relatively small geographic extent. We caution against using the same model in other systems or locations but note that, in general, landscape topographic metrics have been useful for predicting wetland occurrence and explaining variation in flooding dynamics in other regions (Riley et al. 2017; Cianciolo et al. 2021).

In addition to hydrologic metrics, we also used the LiDAR data to estimate vegetation heights for the entire study area. Because long-term fire suppression in pine flatwoods wetlands causes a distinct change in the vegetation structure (Martin and Kirkman 2009), this simple metric provided a way to quantify vegetation characteristics within wetland basins that directly relate to habitat suitability for flatwoods salamanders. Similar methodologies have been used to quantify vegetation characteristics in other wetland systems (Luo et al. 2014), and LiDAR data have been broadly used in various assessments of habitat quality and classification (e.g., Graf et al. 2009; Martinuzzi et al. 2009). Additional collections of LiDAR data could be used to compare changes in vegetation characteristics (or even wetland bathymetries as fire removes duff layers in overgrown wetlands) over time, providing an efficient way to quantify the temporal effects of continued habitat management.

We used assessments of hydrologic characteristics and vegetation structure to broadly delineate potentially suitable flatwoods salamander habitat across our study area. These predictions generally agreed with habitat delineations that were made using expert site knowledge, with some key exceptions. First, mapped habitat was often predicted to occur outside of the areas that we delineated based on existing site knowledge. This was likely caused by a combination of continued habitat improvements from 2016 (field delineations) to 2018 (LiDAR data collection), inability to separate bare ground from short herbaceous vegetation, and the fact that field delineations of habitat are often constrained by our ability to see and access these habitats in fire-suppressed wetlands with dense shrubby overgrowth. Second, there were multiple patches (both field- and LiDAR-delineated) of high-quality vegetation that have been inundated relatively infrequently over the last several years. These areas tended to be closer to wetland edges (Figure 7), which have likely received better fire effects than deeper areas closer to wetland centers (Bishop and Haas 2005). These effects may ultimately force flatwoods salamanders to deposit eggs in areas of wetlands that are less likely to flood, lowering hatching success. However, these areas could play an important role in juvenile or adult salamander ecology as individuals enter and leave wetland basins (Jones et al. 2012). Overall, it can be challenging to assess habitat quality for flatwoods salamanders across a wetland basin via on-the-ground observations, highlighting the need for information describing wetland bathymetry, associated flooding extents, and their relationship with suitable vegetation structure.

While the wetlands in our study area are well-surveyed for flatwoods salamander habitat, broad delineations of potentially suitable habitat across a large number of wetlands could be used to guide management and conservation actions in other parts of the range. In many large wetlands, it can be difficult to identify the best habitat patches without extensive surveys. Identifying potential portions of wetlands to survey before surveyors visit wetlands could increase survey efficiency (Guisan et al. 2006), especially when detection probability is low (Brooks and Haas 2021). These habitat assessments could also be used to identify areas of wetlands where active management (i.e., removal of woody vegetation) would be most effective by expanding existing areas of suitable habitat or focusing efforts on areas of a wetland most likely to be hydrologically suitable. Finally, understanding spatial variability both within and among wetlands could be used to guide ongoing translocation efforts.

Our study was partially limited by the quality of the data that were available. First, and most significantly, 12 of 14 wetland basins with known water levels were partially flooded on the day that the LiDAR data were collected, adding considerable uncertainty to portions of our analyses. This forced us to estimate portions of the stage–area curves in 12 wetlands using well data and to truncate the stage–area curves in 16 wetlands with no well data. Although stage–area curve estimates appeared generally reasonable and were mostly for low water levels, it prevented us from completely mapping wetland bathymetry in most wetlands. Thus, collecting LiDAR data when wetlands are dry is critical for reducing uncertainty and increasing applicability of this approach. Second, many of the topographic metrics used in our analysis were also affected by this uncertainty, making model results less transferable to other pine flatwoods systems and more difficult to interpret. Third, the data that were available did not cover the entire East Bay flatwoods and completely omitted other flatwoods areas with important flatwoods salamander habitat. Together, these issues highlight the need for effective collaboration between the agencies that collect data and scientists on the ground, especially on properties where multiple agencies are working semi-independently (e.g., military bases; Schuett et al. 2001). Fourth, we were unable to assess direct links between flatwoods salamander populations and the habitat metrics delineated in this study. There is currently a lack of spatial data describing salamander populations at a within wetland scale, which is further complicated by the overall rarity of the species (i.e., many wetlands in the study are currently unoccupied).

The methodology and conceptual framework presented here provides ample opportunities for additional research, both for flatwoods salamanders and for other species. There are few studies that examine the effects of within-wetland spatiotemporal variability in flooding on amphibian ecology, fitness, or reproductive success. Larval positioning within a wetland may ultimately impact access to resources, competition, and exposure to predators, especially as wetted areas fragment into multiple patches. Linking either larval growth rates, survival, or size at metamorphosis to conditions experienced by larvae in different portions of a wetland based on flooding regime and access to different habitat types is an important next step. For flatwoods salamanders (and other species laying eggs in dry wetlands), egg positioning may also play an important role in determining reproductive success because hatching depends on both the water level when eggs are laid and subsequent increases in water level that will inundate eggs. Finally, many ephemeral wetlands that provide critical habitat for multiple species are currently being impacted by climate change (Greenberg et al. 2015; Chandler et al. 2016; Davis et al. 2019; Cartwright et al. 2021), potentially reshaping what characterizes a typical period of inundation. Creative applications of remote sensing and field-collected data can allow researchers to better understand hydrologic changes over long time periods or large landscapes (Brice et al. 2022). Ultimately, integrating species ecology with factors controlling hydrologic regimes within wetlands will be fundamental to making informed conservation and management decisions in the face of a changing climate.

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Table 1. Hydrologic and vegetation characteristics measured in pine flatwoods wetlands on Eglin Air Force Base, Florida. All metrics were calculated from high-resolution Light Detection and Ranging (LiDAR) derived elevation data in conjunction with data from hydrological monitoring wells that were available for 14 wetlands. The depth at well and the estimated flooded area refer to the water level and area on the day the LiDAR data were collected. Total areas were delineated in the field and represent each wetland's maximum potential flooded area. Hydroperiod and median flooded area (either observed in wetlands with wells or predicted in wetlands without wells) were calculated across four Reticulated Flatwoods Salamander (*Ambystoma bishopi*) breeding seasons (2015–2019). The FS column denotes presence (1) or absence (0) of flatwoods salamanders within the last 10 years. High-quality vegetation was defined as having a height less than 1.0 m via LiDAR data, and potentially suitable habitat was defined as the intersection of median flooded areas (could not be estimated spatially for one site whose estimated flooded area was larger than the median flooded area) and high-quality vegetation.

ID	FS	Depth at Well (m)	Estimated Flooded Area (m^2)	Mean Hydro-period (days)	Total Area (m^2)	Median Flooded Area (m^2)	High Quality Vegetation (m^2)	Potential Habitat (m^2)
Monitoring Well								
1	0	19.6	793	97	1,905	327	1,231	681
2	0	14.5	1,795	175	10,638	8,661	6,338	4,847
12	0	0.0	0.0	140	17,210	10,327	7,330	3,881
14	0	13.8	2,323	207	6,770	4,996	4,242	3,663
15	1	13.6	2,416	204	35,528	2,472	6,847	803
16	1	12.7	4,196	118	17,128	12,562	6,956	3,709
18	1	19.7	8,300	239	96,595	61,932	20,100	2,405
21	0	0.0	0.0	90	23,821	1,117	8,378	1,001
30	0	12.2	3,453	205	53,346	13,942	25,212	7,028
31	0	18.7	3,433	213	15,593	3,470	6,560	1,772
33	1	11.4	4,689	105	14,702	9,733	9,017	6,833
36	0	7.6	2,988	149	13,757	10,086	6,984	5,169
112	1	32.4	6,520	220	40,966	5,511	4,715	2,950

202	0	13.2	4,052	183	16,787	6,796	5,498	2,173
		No Monitoring Well						
17	0	-	127	-	901	417	174	73
37	0	-	19	-	2,201	1,101	1,469	848
39	0	-	1,610	-	4,064	1,633	2,290	712
113	0	-	1,258	-	18,888	1,692	2,792	79
119	0	-	1,520	-	22,664	7,677	5,480	1,013
200	0	-	64	-	5,236	2,794	912	570
204	0	-	2,978	-	50,137	12,489	15,695	3,356
205	0	-	50	-	33,895	11,854	9,860	1,439
206	0	-	472	-	2,630	1,330	654	262
207	0	-	252	-	833	664	586	463
208	0	-	117	-	40,068	10,358	12,746	2,267
209	0	-	791	-	12,779	5,663	3,985	1,015
210	0	-	494	-	21,635	8,979	1,558	414
230	0	-	149	-	15,783	7,342	9,122	4,129
231	0	-	436	-	50,895	2,345	1,835	53
232	0	-	6,775	-	24,020	5,504	19,017	-

Table 2. Summary statistics for two linear regression models predicting median flooded area of 14 pine flatwoods wetlands during the Reticulated Flatwoods Salamander (*Ambystoma bishopi*) breeding season. Wetlands were located on Eglin Air Force Base, Florida.

	β	SE	t-value	*P*-value
Single-factor Model				
Intercept	0.35	0.066	5.3	0.0002
Wetland Area	-0.13	0.057	-2.3	0.04
Two-factor Model				
Intercept	0.35	0.054	6.5	< 0.0001
Wetland Area	-0.14	0.047	-3.0	0.012
Elevation	0.13	0.051	2.6	0.026

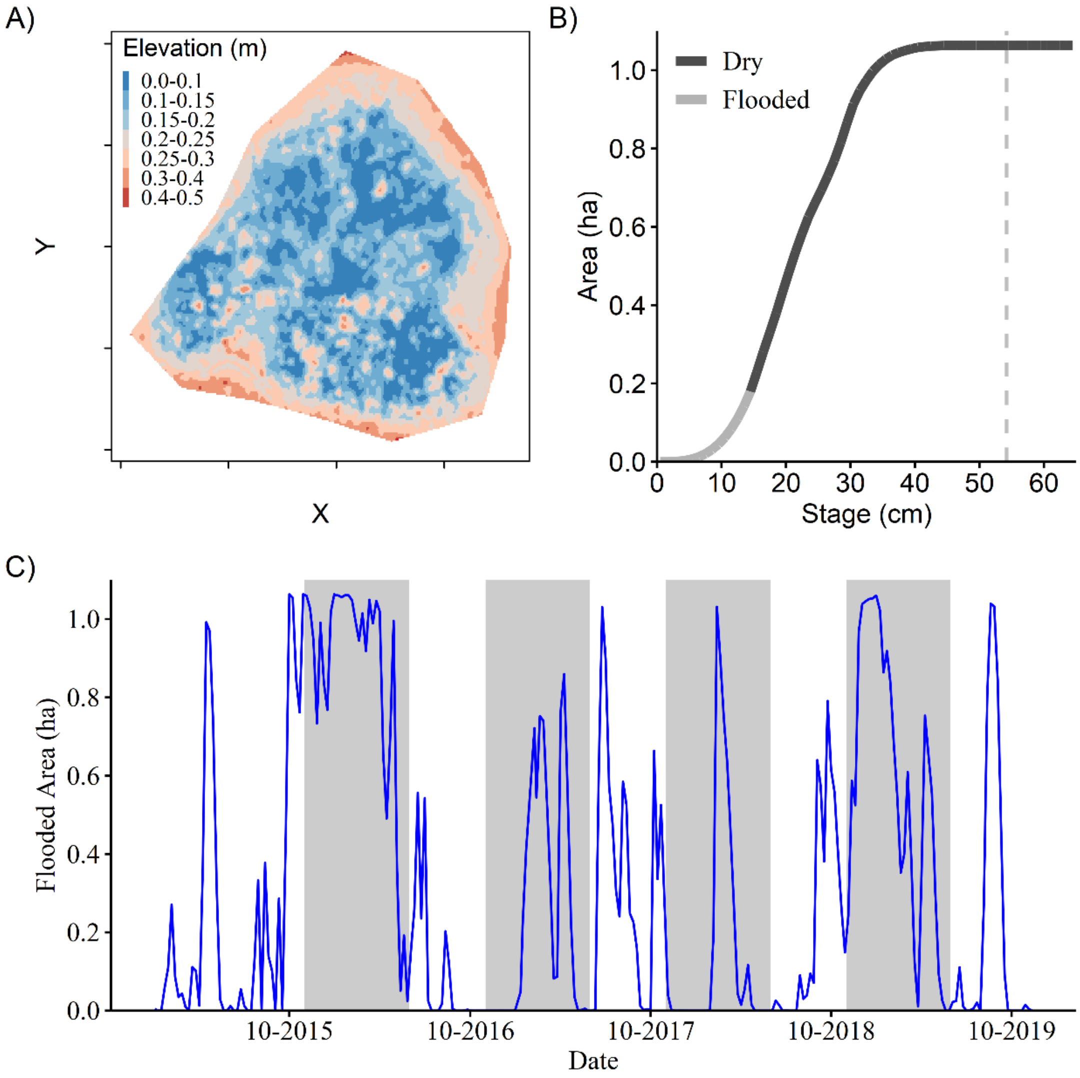

Figure 1. Hydrologic regime in a pine flatwoods wetland (Site 2) located on Eglin Air Force Base, Florida. (A) Wetland bathymetry was calculated using high resolution Light Detection and Ranging (LiDAR) data. (B) Bathymetry was then used to estimate the stage–area relationship for this wetland, using measured (dry pixel elevations during LiDAR collection) and estimated (flooded pixels) data points. The vertical grey line represents the maximum water level that has been recorded at a monitoring well. (C) The stage–area relationship was then used to estimate the daily flooded area for available monitoring well data. Shaded areas represent the Reticulated Flatwoods Salamander (*Ambystoma bishopi*) breeding season (November–May).

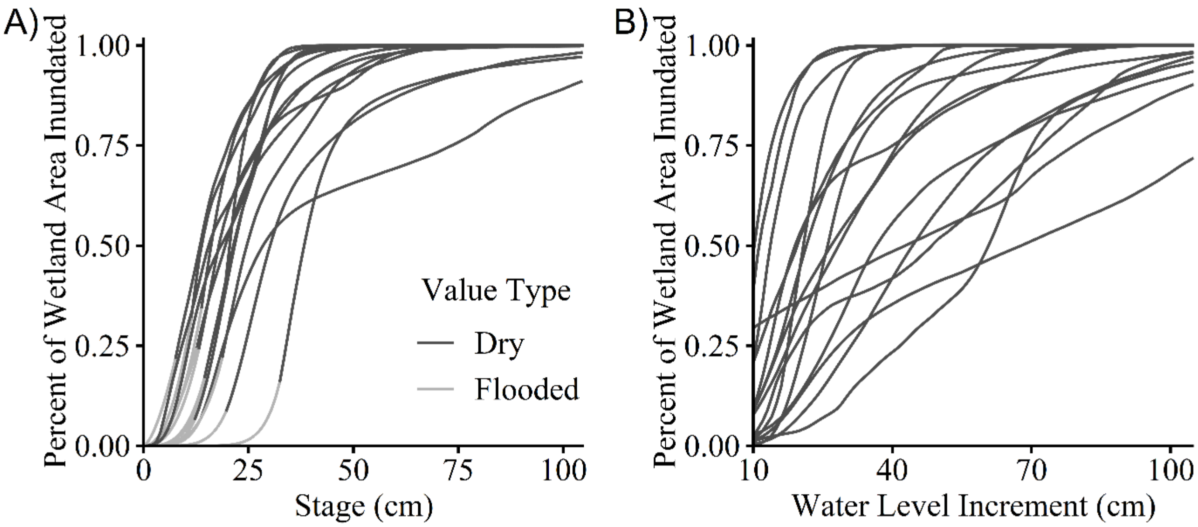

Figure 2. Stage–area relationships for 30 pine flatwoods wetlands on Eglin Air Force Base, Florida estimated from wetland bathymetry data. (A) Some wetlands (n = 14) contained monitoring wells when the Light Detection and Ranging (LiDAR) data were collected, and the portions of the stage–area curve that were predicted to be underwater during data collection (i.e., flooded) were estimated using a power function, data from dry pixels, and known water depth at the time of LiDAR collection. (B) Other wetlands did not contain monitoring wells, and these relationships are represented by increasing water level increment above the lowest elevation in the wetland based on the LiDAR data. Elevations < 0.1 m above the lowest elevation were omitted because of the likely presence of water in the wetland basin.

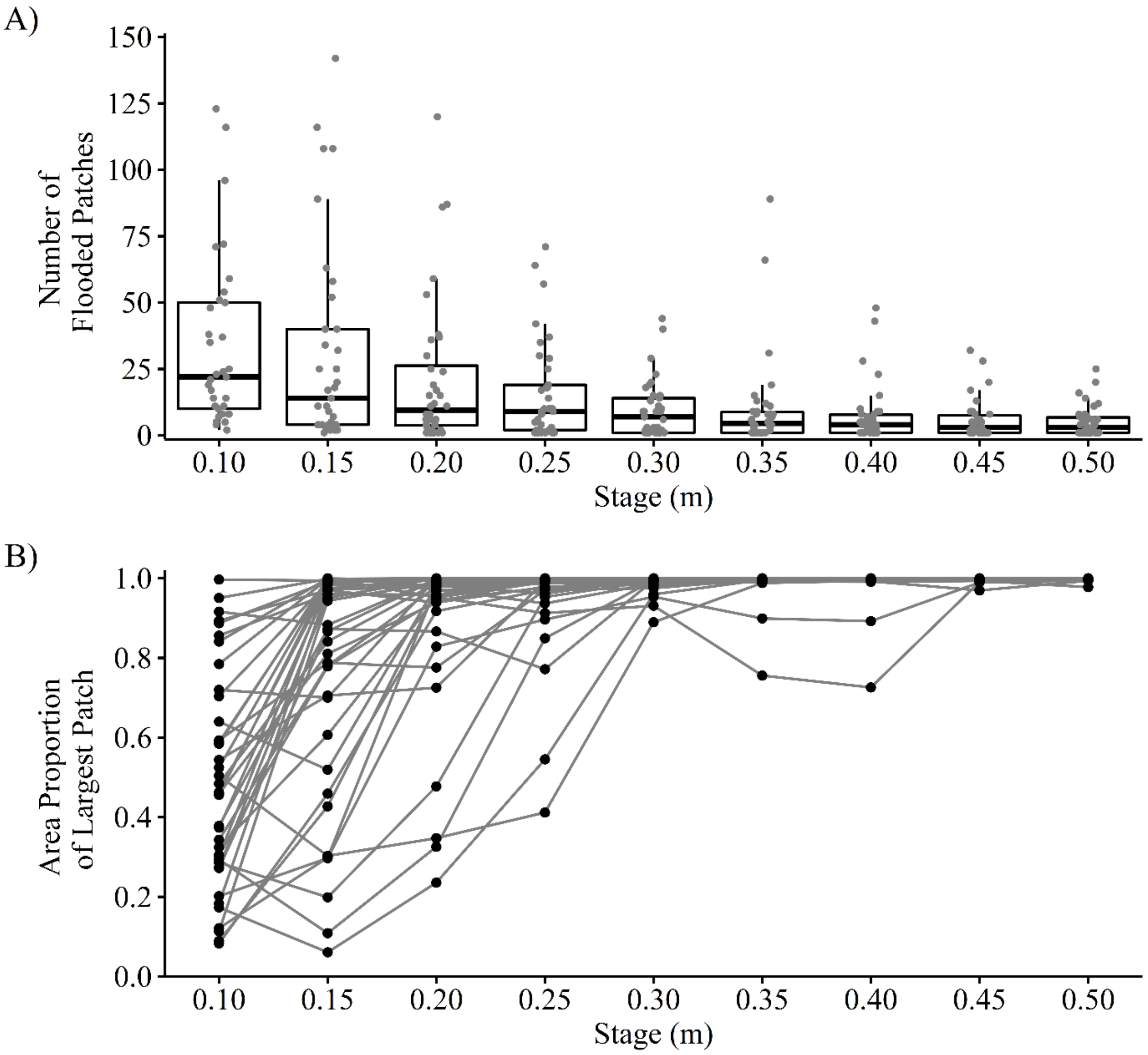

Figure 3. Flooded areas in 30 pine flatwoods wetlands on Eglin Air Force Base, Florida as water level (stage) increases. (A) The number of discrete flooded patches with an area greater than one m^2 across 30 wetlands (each point represents the number of patches in a single wetland). Twelve points > 150 patches not shown on plot (max = 833). (B) The percentage of the total flooded area represented by the largest patch (each line represents a single wetland).

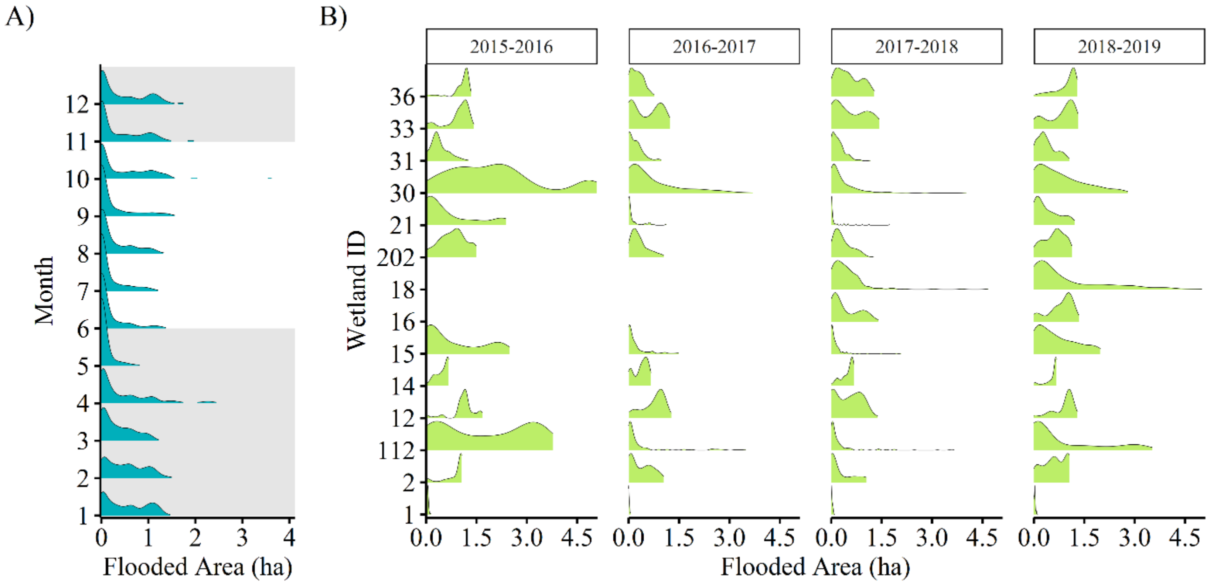

Figure 4. Density plots showing the distribution of flooded areas in 14 pine flatwoods wetlands from 2015–2019. (A) Flooded areas are pooled across wetlands and plotted monthly and (B) for individual wetlands during the Reticulated Flatwoods Salamander (*Ambystoma bishopi*) breeding season (November–May, shaded in A). All wetlands were located on Eglin Air Force Base, Florida.

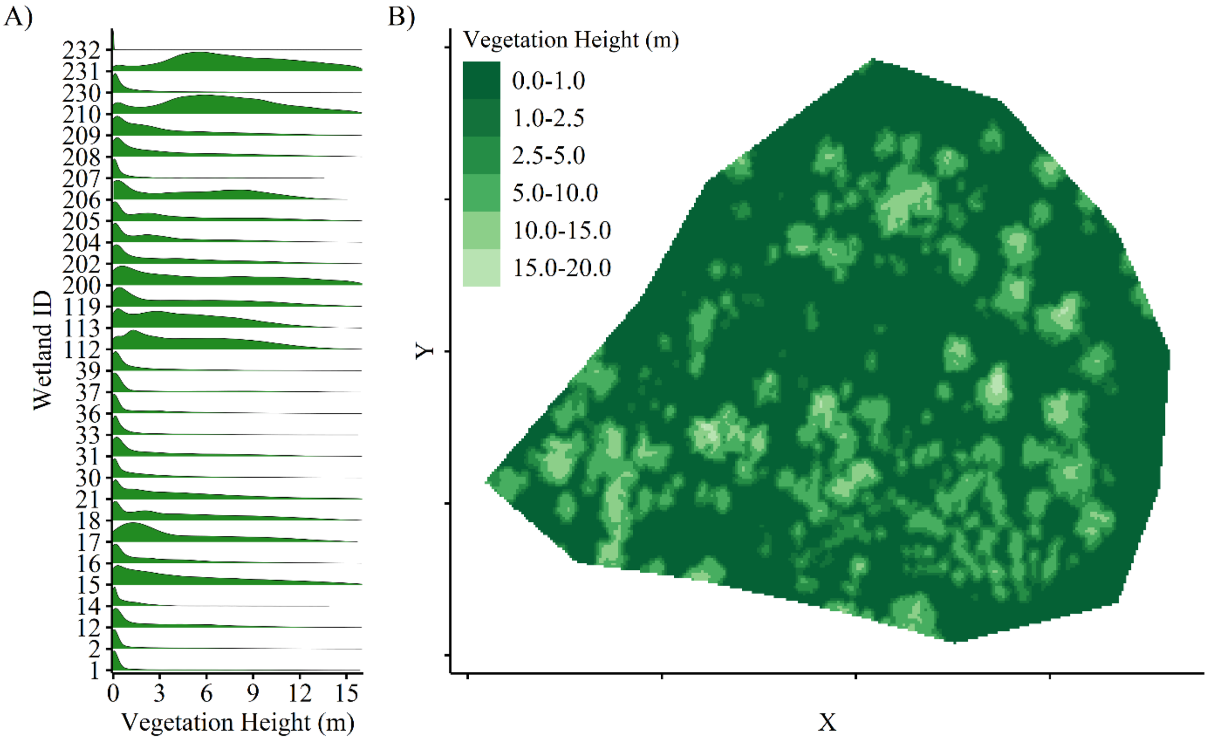

Figure 5. (A) Density plots showing the distribution of vegetation heights in field-delineated pine flatwoods wetlands on Eglin Air Force Base, Florida. (B) Vegetation structure in pine flatwoods wetlands is characterized by extensive areas of herbaceous vegetation (vegetation heights typically less than one m) with overstory trees (heights generally > 10 m) and woody vegetation (heights approximately 2.5–10 m) scattered throughout the wetland basin.

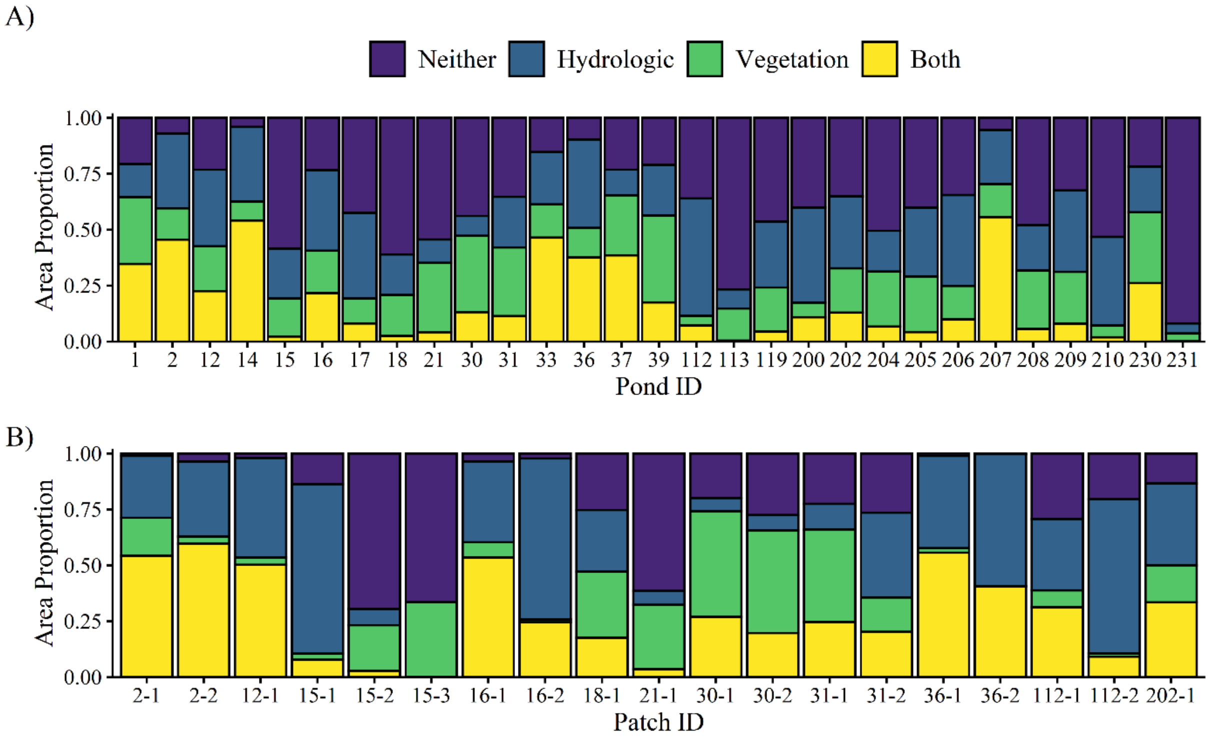

Figure 6. The amount of wetland habitat predicted to be suitable for Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) in wetlands on Eglin Air Force Base, Florida. Wetland habitat was classified as having suitable hydrology (i.e., flooded 50% of the time during the flatwoods salamander breeding season; shown in blue), vegetation (i.e., less than 1.0 m high; shown in green), or both (shown in yellow) based on remotely sensed Light Detection and Ranging (LiDAR) data. (A) The percentage of each habitat type delineated with LiDAR-based assessments within each wetland. (B) The percentage of habitat types within patch areas (delineated by a 1, 2, or 3 after the wetland ID) that were delineated in the field as being suitable for flatwoods salamanders.

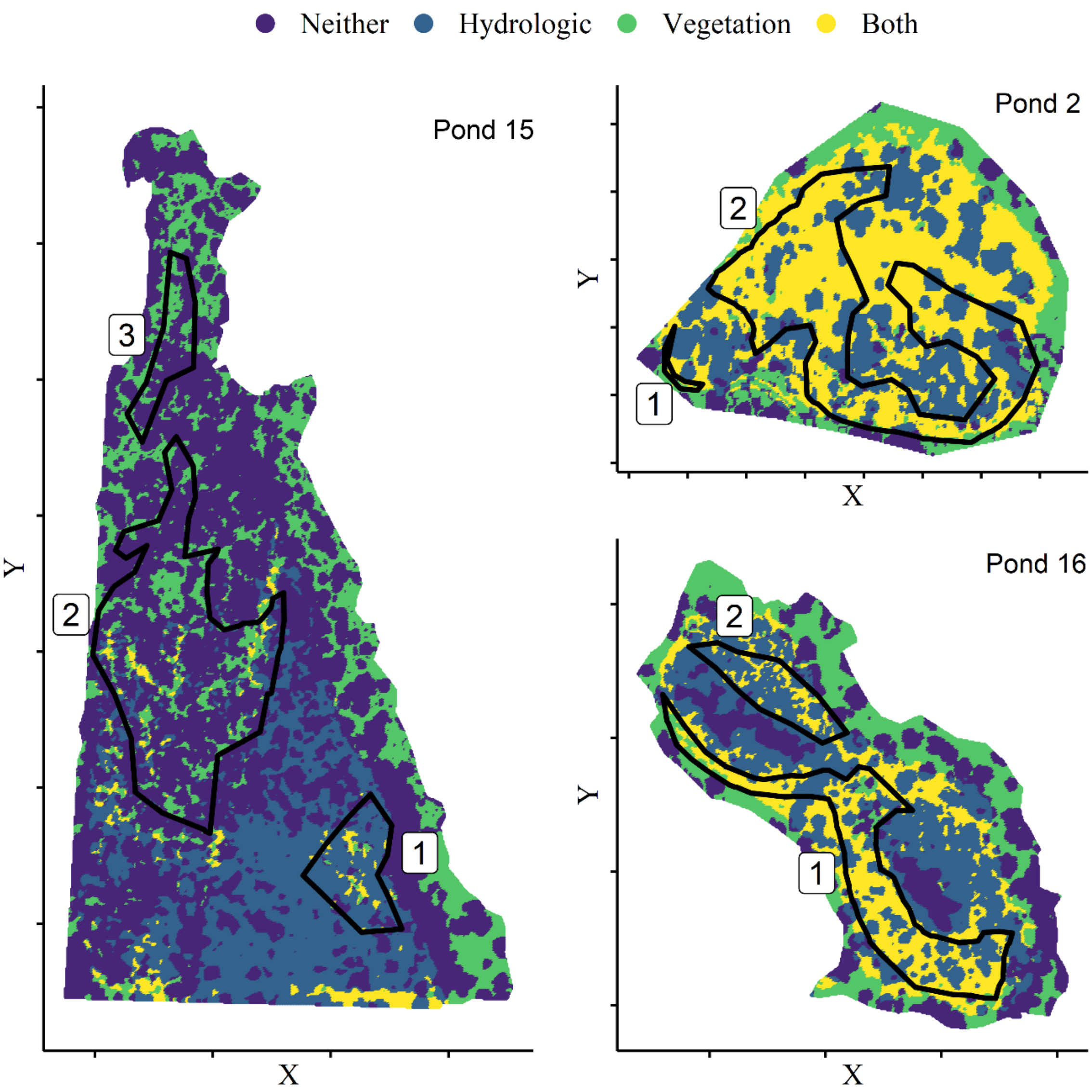

Figure 7. Potentially suitable habitat for Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) in three pine flatwoods wetlands on Eglin Air Force Base, Florida. Potential habitat was defined by areas of high-quality vegetation (i.e., less than 1.0 m high), high-quality hydrology (i.e., flooded 50% of the time during the flatwoods salamander breeding season), or both. These metrics were derived using remotely sensed Light Detection and Ranging (LiDAR) data in conjunction with hydrologic monitoring well data. Black lines represent areas that were field delineated as having high-quality vegetation for flatwoods salamanders.

CHAPTER 2

Wetland hydrology, not phenological shifts, challenges Reticulated Flatwoods Salamander (*Ambystoma bishopi*) management under future climate change

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Abstract

Shifts in phenology have been one of the most frequently documented effects of climate change across a wide variety of taxonomic groups. These shifts can alter both species and ecosystem level processes, and for species of conservation concern, may impact the effectiveness of ongoing management programs. Here, we used 10 years (2010–2020) of drift fence data to quantify the breeding phenology of the endangered Reticulated Flatwoods Salamander (*Ambystoma bishopi*) at two breeding wetlands in Florida. We then used downscaled climate projections from three Global Circulation Models (GCMs; Hadley Centre Global Environment Model 2 Earth Systems, Hadley Centre Global Environment Model 2 Carbon Cycle, and the Community Climate System model version 4) each with two emission scenarios to forecast how flatwoods salamander breeding phenology may change from 2030–2099. We combined these forecasts with an existing hydrologic model that was built using the same climate data to examine how wetland hydrology and phenology may interact to impact salamander recruitment in future years. We found that large movements (≥ 5 individuals) of adult salamanders moving into breeding wetlands were tightly linked to precipitation events with minimum temperatures above freezing, while juvenile emigration was less strongly tied to precipitation and occurred on more days than adult immigration. Under all six GCM-emission scenario combinations, only one scenario suggested that there would be fewer immigration opportunities by the year 2099, and two scenarios (both high emission) indicated that the timing of immigration may shift to later in the fall breeding period. All projections predicted few years will have an ideal intersection of phenology and hydrology for flatwoods salamander reproduction but that many years would have marginal conditions where recruitment may still be possible. Because the frequency of successful breeding years affects population viability in flatwoods salamanders, ongoing

management programs must ensure that populations are reproducing frequently enough to remain viable. Overall, our results indicate that altered wetland hydrology (e.g., shorter hydroperiods during the breeding season) and other effects of climate change (e.g., sea level rise) are more likely to contribute to flatwoods salamander declines over the next several decades than phenological shifts.

Introduction

Predicting how natural communities will respond to climate change has been a common theme in conservation biology for many years (McCarty 2001; Hannah et al. 2002), with climate change projected to have significant effects on biodiversity (Sala et al. 2000) and a host of fundamental ecological and evolutionary processes (Walther et al. 2002; Parmesan 2006). For species whose physiology, habitat requirements, or life history traits depend on a specific set of climate parameters, a changing climate may necessitate some type of adaptive change, plasticity in traits, or dispersal into new habitats to ensure long-term population stability (Foden et al. 2013; Thurman et al. 2020). Without such responses, some species may be pushed towards extinction as environmental characteristics become unsuitable (McCarty 2001; Thomas et al. 2004). Thus, developing a better understanding of how environmental changes will impact the ecology of imperiled species is a critical research need.

Shifts in phenology, the timing of life history events, as a response to ongoing climate change have been documented in a wide range of taxa, including mammals (Lane et al. 2012), birds (Koleček et al. 2020), insects (Roy and Sparks 2000), amphibians (Todd et al. 2011), fish (Lynch et al. 2016), and plants (Cleland et al. 2007). However, shifts in phenology are not uniform across taxa, regions, or seasons (Walther et al. 2002), and responses to climate change involve complex interactions between a species' ecology and regional climate patterns. Variation in phenology can alter fitness and reproductive success (Dickey et al. 2008; Linton and Macdonald 2017; Farzan and Yang 2018) or create asynchrony between important interspecific or ecological interactions (Visser and Holleman 2001; Simmonds et al. 2020). Responses to climate-induced changes in phenology can have both positive and negative effects on population-level processes (Iler et al. 2021), leading to uncertainty when predicting how climate change will impact ongoing management efforts.

Amphibians breeding in ephemerally flooded wetlands typically make seasonal migrations from surrounding uplands into wetland basins as a response to environmental cues (Semlitsch 1985; Cook et al. 2006; Todd and Winne 2006; Plenderleith et al. 2018). Previous research indicates that shifts in amphibian breeding phenology have already occurred in some species because of changing temperature and/or precipitation patterns (e.g., earlier breeding in spring and later breeding in fall; Gibbs and Breisch 2001; Todd et al. 2011), although shifting phenologies are not ubiquitous across amphibian taxa (Blaustein et al. 2001). Shifting migration dates may have cascading effects on the overall reproductive output of pond-breeding amphibians. For example, Bernard (2015) found that earlier breeding was related to lower female fecundity in female Wood Frogs (*Rana sylvatica*), and breeding date significantly altered the duration of the larval period. In fact, changes to larval habitats caused by either the timing of reproduction or direct climate effects (e.g., warmer temperatures or altered wetland hydrology), can alter growth, development, and survival of larval amphibians (Mills and Barnhart 1999; Duarte et al. 2012; Walls et al. 2013). Moreover, environmental factors experienced by larval amphibians can interact in non-additive ways to impact larval survival until metamorphosis (O'Regan et al. 2014). Taken together, these studies indicate that climate change is likely to have complex effects on pond-breeding amphibian populations, with multiple threats to fitness and population viability (Blaustein et al. 2010).

Reticulated Flatwoods Salamanders (*Ambystoma bishopi*), small ambystomatid salamanders endemic to the southeastern United States, exemplify the challenges faced by pond-breeding amphibians under a changing climate, experiencing threats from altered wetland hydrology (Chandler et al. 2016), large storm events (Walls et al. 2019), and rising sea levels (USFWS 2020). These threats are exacerbated by both historic and ongoing range contractions and populations declines (USFWS 2009; O'Donnell et al. 2017). Despite known links between flatwoods salamander breeding migrations, temperature, and precipitation (Brooks et al. 2019), no research has examined how climate change may impact flatwoods salamander phenology even though these relationships could affect ongoing management programs. Adult flatwoods salamanders lay eggs terrestrially in wetland basins (Anderson and Williamson 1976) and, thus, face a tradeoff of arriving at wetlands too early and risking egg desiccation before wetlands fill versus arriving too late and laying eggs in parts of the wetland basin that have a lower probability of being inundated later in the breeding season. If flatwoods salamander breeding migrations shift to occur later in the fall, as has been documented with other fall-breeding salamanders, including the terrestrial egg laying Marbled Salamander (*A. opacum*; Todd et al. 2011), it could have multiple effects on reproduction, fitness, and population viability.

Here, we used a 10-year record (2010–2020) of flatwoods salamander movement data from Eglin Air Force Base, Okaloosa County, Florida to quantify the phenology of adult immigration and metamorph emigration from two breeding wetlands. We identified environmental conditions (e.g., precipitation and temperature patterns) that were conducive to adult movements into wetlands and assessed how these conditions may change as a response to climate changes that are projected to occur in this region. Our goal was to address whether the frequency or timing of potential movement opportunities would change in future years. We then integrated predictions about flatwoods salamander phenology with pond-specific hydrologic predictions made by Chandler et al. (*In prep*) to identify potential mismatches in movement cues and wetland hydrology. Understanding the potential magnitude of phenological shifts and how they may interact with changes in hydrology will allow managers to prioritize management actions that minimize the effects of climate change on flatwoods salamander populations.

Methods

Study Sites

We sampled flatwoods salamanders at two breeding wetlands on Eglin Air Force Base (AFB) in Okaloosa County, Florida from 2010–2020 (10 breeding seasons). Eglin AFB is a large military installation located in the Florida Panhandle that contains over 145,000 ha of actively managed Longleaf Pine forests. Both breeding sites are small (0.45 and 0.36 ha) pine flatwoods wetlands characterized by an understory of thick herbaceous vegetation with a pine overstory that was historically maintained by regular growing-season fires (Bishop and Haas 2005). Today, vegetation structures have been maintained through a combination of mechanical treatments to remove woody vegetation and the application of prescribed fire (Gorman et al. 2013). Eglin AFB has an active fire management program that has improved and maintained the landscape surrounding breeding sites as one of the best remaining examples of the pine flatwoods ecosystem.

Salamander Sampling

We captured salamanders immigrating into and emigrating from breeding wetlands using drift fences that completely encircled each wetland. We constructed drift fences from 60-cm high rolls of galvanized steel flashing that were partially buried (15–20 cm) to reduce trespass under the fence. We positioned paired (one inside and one outside) aluminum-mesh funnel traps (85 x 20 cm) approximately 10 m apart along each fence. We placed a wet sponge inside of each trap and a shade board over top of the trap to reduce the chances of unintended mortality events. Additional details of the drift fencing methodologies can be found in Erwin et al. (2016).

The exact timing that drift fences were in operation varied from year to year, but we generally opened traps during the fall (i.e., late September through November). We attempted to open traps no later than the first weather conditions that were conducive to salamanders immigrating into wetlands. We seldom ran drift fences continuously through the entire breeding season and often closed fences during late winter and early spring if metamorphosis seemed unlikely because of dry wetlands. However, in the years when hydrologic conditions were conducive to metamorph emergence from breeding wetlands, we attempted to run fences continuously during the spring emergence period. Thus, the period and number of nights drift fences were operational changed each breeding season depending on staff availability, weather conditions, and the hydrology of the breeding wetlands (Appendix B: Table S1). When fences were operational, we checked fences at least twice a day (morning and evening), with the number of checks increasing depending on weather conditions (e.g., warm rainy nights; Erwin et al. 2016). We closed traps and removed sections of each fence when the fences were not operational to allow animals to move into and out of the wetlands.

We marked all flatwoods salamanders using either a passive integrated transponder (PIT) tag or visual implant elastomers (VIE). We also measured the snout-vent length (SVL) of all captured salamanders. We released all salamanders on the opposite side of the drift fence from their capture locations.

Environmental Data

To describe conditions during the contemporary period (2010–2020), we downloaded climate data from the PRISM Climate Group (https://prism.oregonstate.edu, created 11 November 2021). For each breeding season, we obtained daily precipitation and minimum temperature data using the centroid of each breeding wetland as the basis for interpolation, which factors in values from surrounding grid cells through inverse-distance squared weighting (Daly et al. 2008). We chose this dataset to describe contemporary conditions because detailed, site-specific data were not available for all 10 breeding seasons and because previous analysis has indicated that the PRISM datasets are highly correlated with data measured at our study sites in recent years (Brooks et al. 2019).

To characterize a range of potential future climate conditions, we downloaded statistically downscaled climate data for the period of 2030–2099 (70 flatwoods salamander breeding seasons). We selected three Global Circulation Models (Hadley Centre Global Environment Model 2 Earth Systems [HadGEM2-ES], Hadley Centre Global Environment Model 2 Carbon Cycle [HadGEM2-CC], and the Community Climate System model version 4 [CCSM4]) that were each downscaled to 6 x 6 km grids using the Localized Constructed Analogs (LOCA) method (Pierce et al. 2014). For each GCM, we obtained data for two representative concentration pathways (RCPs): 4.5 (assumes peak carbon emissions occur in 2040; Thomson et al. 2011) and 8.5 (assumes carbon emissions continue to increase until 2100; Riahi et al. 2011). Each dataset consisted of daily maximum and minimum temperature (°C) and daily precipitation (mm) data, and both study sites were contained within a single 6-km grid cell. Thus, our final climate dataset consisted of six GCM-RCP combinations, with the same forecasted values for each wetland.

Data Analysis

We focused our analyses on two specific types of salamander movement: adult immigration into the breeding wetlands and metamorph emigration out of the breeding wetlands. For analysis of adult immigration, we removed all juvenile and subadult salamanders from the dataset, defining adult salamanders as any individual that could potentially reproduce based on the SVL of the smallest documented gravid female (46.7 mm) (Haas, unpublished data). We then identified the first instance that each individual was captured entering the drift fence (immigrating into wetlands) in every breeding season and removed all subsequent captures (i.e., each individual was only counted once per season). We also excluded all captures of individuals that were never captured entering the wetland in a particular breeding season (i.e., individuals that trespassed the drift fences or moved into wetlands when the fences were not operational). For analyses focusing on metamorph emigration, we included all captures of salamanders that were identified as metamorphs based on their size and lack of adult pattern, as well as the time of year (late March to early June). We then followed a similar procedure, excluding all capture events after the initial capture within a single season and all captures of individuals that were only captured entering the wetland. Finally, we summarized capture events of both age groups as the total number of individuals captured in each 24-hour period, which we defined as occurring from 12:00–12:00 (i.e., all salamanders moving after midnight were assigned to the previous day’s total).

To examine the potential effects of climate change on adult salamander immigration into breeding wetlands, we identified all movement opportunities in each breeding season from 2030–2099 that fell within the bounds of observed phenological variation over the last 10 breeding seasons. We initially conceptualized movement opportunities as occurring during precipitation events (Brooks et al. 2019). We included the day before precipitation began within each precipitation event and ended each movement opportunity on the final day of precipitation that was followed by at least three consecutive dry days. Across each period, we summed the total number of individuals captured, calculated the total amount of precipitation, and calculated the mean minimum daily temperature. We then refined our definition of movement opportunities using data from 2010–2020, focusing on concentrated movements of at least five individuals (either across a precipitation event or on a single dry day). We refer to these as large movements throughout. We identified the earliest and latest dates and the lowest and highest mean minimum temperature of large movements in our dataset. Thus, movement opportunities for adult immigration (i.e., periods with conditions observed during large movements) were defined as precipitation events occurring from October 13 to December 31 and with mean minimum temperatures ranging from 5.325–20.85°C. Using this definition, we calculated the number of movement opportunities during each breeding season for all six GCM-emission scenario combinations. For each scenario, we tested for differences in the number of movement events per season across each decade using an Analysis of Variance (ANOVA) and used Tukey's HSD to test for differences between *post-hoc* comparisons when the ANOVA was significant. We also tested for temporal shifts in movement opportunities with a series of linear regression models using the Julian date of the 1st and 4th movement opportunity (but used the 2nd or 3rd opportunity in years without four movement opportunities) in each breeding season.

Finally, we forecasted conditions that may occur in each flatwoods salamander breeding season by combining the results of the above phenology analyses with the hydrologic predictions made in Chandler et al. (*In prep*). Briefly, Chandler et al. (*In prep*) made site-specific daily water level predictions for the two breeding wetlands examined in this study using a multi-year history of water level and climate data and the same climate models described above. We scored each salamander breeding season based on multiple characteristics that could impact flatwoods salamander reproductive success. First, we classified all breeding years based solely on their hydrologic suitability (i.e., the longest predicted hydroperiod) during the flatwoods salamander breeding season (October–May). Years with a hydroperiod shorter than 11 weeks were deemed unsuitable based on the minimum time needed to complete the larval period (Palis 1995). We then split years with a suitable hydroperiod into two categories (an 11–15 week or 15+ week hydroperiod) because the length of the larval period has a significant impact on size at metamorphosis (i.e., short and ideal hydroperiod scenarios; Brooks et al. 2020). Second, for all years with a suitable hydroperiod, we identified how periods of inundation interacted with predicted immigration and emigration windows. For immigration, we identified whether wetlands were inundated during salamander movement opportunities (i.e., wetlands flooded at immigration causing salamanders to deposit terrestrial eggs higher in the wetland basin, likely lowering hatching success) or whether the wetland filled and dried during or after immigration but prior to the longest hydroperiod (i.e., potentially causing larval mortality). For all assessments, we defined immigration windows as occurring from the 1st to the 4th movement opportunity but used the 2nd or 3rd opportunity in years without four movement opportunities. For emigration, we identified whether early filling following by early wetland drying would allow for a sufficient hydroperiod but force salamanders to metamorphose and emigrate during the winter, which is outside of the observed period when metamorphs have been documented in the field (i.e., prior to March 15; labeled as winter metamorphosis). This resulted in six potential outcomes, including 1) unsuitable, 2) winter metamorphosis, 3) flooded at immigration, 4) flooding and drying, 5) short hydroperiod, or 6) ideal.

Results

Observed Phenology

From 2010–2020, 49 large movements (≥ 5 individuals) of adult flatwoods salamanders accounted for approximately 75% (636 of 853) of all documented immigration into breeding wetlands. These movements occurred between October 13 and December 31 (80% of all October–December immigration), with small numbers of salamanders continuing to enter wetlands after all large movements had occurred (Table 1). All but two (96%) large movements (7 and 6 individuals) coincided with a precipitation event. Furthermore, adult salamanders were most likely to immigrate into wetlands either the day before precipitation started or the first day of the precipitation event (Figure 1A). On average, all large movements of adult salamanders into breeding wetlands occurred by 4.1 ± 2.4 (SD) precipitation events with suitable temperatures (range: 1–8 precipitation events; Table 1).

We documented successful reproduction and metamorphosis during five breeding seasons at one site and during four seasons at the other site. However, only three breeding seasons (2013–2014, 2015–2016, 2016–2017) were characterized by large metamorph emigration events that were suitable for examining trends in salamander phenology (Table 2). Across these three breeding seasons, emigration occurred from late March through the end of May, with large movements of metamorphs happening over an approximately 5-week period from March 28 to May 3. Emigration events coincided with wetland drying and low water levels in 2016 and 2017, but salamanders emigrated from wetlands during 2014 while water levels were still high (Figure 2). Overall, large movements of metamorphs were less strongly tied to precipitation than adult immigration (Figure 1), and metamorph emergence occurred on an average of 24.4 days per season (compared to an average of 14.8 days per season with any adult immigration).

Phenology under Future Climate Scenarios

Across all six GCM-emission scenario combinations, there were consistent movement opportunities for flatwoods salamanders that fell within currently observed phenological variation (Figure 3). We observed no significant differences in the number of potential movement opportunities across decades in five of six climate scenarios (HadGEM2-CC RCP 4.5: $F_{6,63} = 0.79$, $P = 0.58$; HadGEM2-ES RCP 4.5: $F_{6,63} = 0.36$, $P = 0.9$; HadGEM2-ES RCP 8.5: $F_{6,63} = 1.15$, $P = 0.35$; CCSM4 RCP 4.5: $F_{6,63} = 0.20$, $P = 0.98$; CCSM4 RCP 8.5: $F_{6,63} = 1.66$, $P = 0.15$). The only exception was the HadGEM2-CC RCP 8.5 scenario ($F_{6,63} = 3.21$, $P = 0.008$), which had, on average, fewer predicted movement opportunities in the 2090s than in either the 2050s or 2060s ($P = 0.03$ and 0.01, respectively). Predicted conditions during movement opportunities were highly variable, but daily minimum temperature tended to increase over time by approximately 0.5–2.0°C depending on the GCM and emission scenario (Appendix C: Table S1). Similarly, the predicted timing of potential movement opportunities was variable through time and across scenarios (Figure 4). However, there were consistent shifts towards later immigration opportunities in both the HadGEM2-CC 8.5 (1^{st}: $F_{1,68} = 20.4$, $P < 0.001$; 4^{th}: $F_{1,62} = 16.3$, $P < 0.001$) and HadGEM2-ES 8.5 (1^{st}: $F_{1,68} = 30.1$, $P < 0.001$; 4^{th}: $F_{1,62} = 10.2$, $P = 0.002$) scenarios. These trends corresponded to a later shift of approximately 2.6–3.6 days per decade (Table 3). All other scenarios produced non-significant temporal trends (Table 3).

Using a combination of phenology predictions, site-specific hydrologic models, and GCMs, we scored future breeding seasons based on their potential suitability for flatwoods salamander reproduction (Figure 5, Appendix C: Figures S1–S2). As expected, results were both temporally variable and variable across GCM-emission scenarios (Appendix C: Table S2, Figures S1–S2), but some major trends were apparent. First, approximately 19–54% of years were predicted to be unsuitable based on hydroperiod alone, and the number of unsuitable years was relatively similar across emission scenarios for each GCM. Second, hydrology was frequently predicted to negatively interact with phenology. At immigration, approximately 4–20% of years were predicted to have flooded wetlands during the entire immigration period, and approximately 24–57% of years were predicted to experience flooding and drying before the longest hydroperiod. At metamorphosis, the timing of drying events was predicted to force salamander larvae to exit wetlands earlier than has been observed in natural populations in approximately 11–31% of years. Overall, the predictions indicated that approximately 3–17% of breeding seasons from 2030–2099 are likely to have the ideal intersection of phenology and hydrology for flatwoods salamander reproduction.

Discussion

We used 10 years of drift fence data documenting flatwoods salamander movements into and out of breeding wetlands to examine how climate change may impact the phenology of this imperiled species. Across six GCM-emission scenario combinations, we found little evidence that the environmental conditions triggering adult flatwoods salamander immigration into breeding wetlands will shift outside of currently documented phenological variation by the year 2099. Only the high emission scenario for the HadGEM2-CC model indicated potentially fewer movement opportunities by the end of the 21st century. We found more support for a potential shift in movement opportunities that would delay immigration to later in the breeding season (occurred in the high emission scenario for the HadGEM2-CC and HadGEM2-ES model). A potential shift to later arrival of adult salamanders is similar to trends that have been reported for other fall-breeding amphibians (Todd et al. 2011) and, more broadly, in fall phenological responses to climate change (Walther et al. 2002; Gill et al. 2015; Pearson 2019). Later arrival and breeding of adult flatwoods salamanders could ultimately constrain the larval period in some years, although this variation would still be within the timeframe when large movements of adult salamanders have been observed in recent years. All three significant trends in phenological forecasts occurred under high emission scenarios, and the magnitude of any future shifts in phenology will depend, at least in part, on the severity of global climate changes experienced by salamander populations at a local scale (i.e., exposure; Dickinson et al. 2014).

By combining phenological predictions with an existing hydrologic model (Chandler et al. *In prep*), we were able to forecast potential breeding conditions for two flatwoods salamander populations, allowing us to examine broad trends across future years. These predictions clearly indicate that few breeding seasons are likely to have an ideal intersection of phenology and hydrology (regardless of the GCM-emission scenario combination), which is similar to observations from recent years (i.e., 1–2 ideal breeding seasons in 10 years). While conditions that are unsuitable for reproduction (i.e., too dry) were predicted to occur frequently, most breeding seasons will likely be characterized by marginal environmental conditions that could still allow for recruitment. Hydroperiods ranging from 11–15 weeks are sufficient for larval development (Palis 1995) but decrease size at metamorphosis (Brooks et al. 2020). This may have important impacts on population dynamics because metamorph body size has been shown to effect multiple aspects of adult fitness in ambystomatid salamanders (e.g., survival and age at first reproduction; Semlitsch et al. 1988; Scott 1994; Brooks 2020). Flooded wetlands during immigration and flooding and drying prior to the longest hydroperiod can both negatively impact reproductive success (e.g., egg hatching or larval survival rates). However, it is difficult to predict and quantify the magnitude of these effects, which could range from complete reproductive failure to only small-scale impacts on reproduction (which have both been observed in recent years), depending on water levels and the timing of events. Intermittent water levels could be mitigated if flatwoods salamander larvae can persist through short dry periods by sheltering underground (i.e., in crayfish burrows; Heemeyer et al. 2012; Powell et al. 2015; Bloomer et al. 2021), but field data demonstrating this ability are lacking. Finally, perhaps the most important interaction between phenology and hydrology identified here is that wetland drying will often force metamorphosis earlier than it has been observed in wild flatwoods salamander populations (i.e., late March; Means 1972; Erwin et al. 2016). It is unclear if earlier metamorphosis is physiologically possible for flatwoods salamanders under natural conditions, although warming trends could increase larval growth rates and shorten times to metamorphosis (Keen et al. 1984; O'Regan et al. 2014). Ultimately, the viability of flatwoods salamander populations is affected by the frequency of years with successful recruitment (Brooks 2020), suggesting that reproductive success during years where phenology and hydrology combine to produce marginal conditions will be an important aspect of flatwoods salamander population demography in future years.

At our study sites, adult flatwoods salamanders demonstrated substantial temporal variation in movement events over the last 10 breeding seasons, both within and across years. Within an individual breeding season, adult salamanders frequently arrived at breeding wetlands in multiple movement pulses over an extended period each fall, and similar immigration patterns have been documented in other ambystomatid salamanders (e.g., Semlitsch 1985; Semlitsch and

Anderson 2016). The ultimate drivers of this variation are unclear but could be related to varying responses to environmental cues, differences in travel times to breeding sites, selection pressures for both early and late breeding, or energetic differences (i.e., some individuals may not be ready to breed until later in the year) (Harris 1980; Stenhouse 1985; Scott et al. 2013). Regardless of the mechanisms involved, we note that this type of variability could serve as a form of bet-hedging in flatwoods salamander populations. In some years, arriving early in the breeding season may be advantageous (if wetlands fill soon after arrival and remain flooded for several months), while in other years, arriving later could be advantageous (if hydroperiods are intermittent early in the season or if wetlands are flooded early in the season before drying down to expose more egg laying habitat). Thus, there may be selection pressure for both early and late arrival dates across the entire salamander population because of the inherent annual hydrologic variability in these systems (Harris 1980).

From 2010–2020, large movements of adult flatwoods salamanders into breeding wetlands were tightly linked to precipitation events with temperatures above freezing. Similar conditions have been previously suggested to drive immigration in both flatwoods salamanders (Palis 1997; Brooks et al. 2019) and other ambystomatid species (e.g., Hardy and Raymond 1980; Sexton et al. 1990; Semlitsch and Anderson 2016). Our analysis indicated that adult salamanders commonly began arriving at breeding wetlands either the day before or the first day of a precipitation event. While mismatches in the temporal scale of salamander and precipitation data (i.e., hourly vs. daily) make it challenging to make fine-scale predictions of salamander movements (Semlitsch 1985), our data suggest that salamanders may be responding to environmental cues other than precipitation to initiate movements (e.g., declines in barometric pressure; St. Andre 2012). Large salamander movements occurred over a wide range of temperatures and appeared to be limited more frequently by freezing temperatures than by high temperatures. One of the most consistent trends in our forecasts was, unsurprisingly, increasing temperatures over the next several decades. These changes will, on average, remain within the temperature range observed during immigration events in recent years, but it is possible that long-term temperature increases will ultimately exceed some threshold that could limit flatwoods salamander surface activity (Gatz 1970; Peterman and Semlitsch 2014). Furthermore, warming temperatures could impact a variety of other demographic (e.g., adult survival, egg hatching rates, growth rates, and metamorph survival; Trenham et al. 2000; Rothermel and Semlitsch 2006) and environmental processes (e.g., wetland hydrology; Chandler et al. 2016). Ultimately, these other potential effects of rising temperatures on salamander populations appear more likely to influence salamander population dynamics than temperature effects on movement phenology.

While the two flatwoods salamander populations discussed here are well-studied (e.g., Erwin et al. 2016, Brooks et al. 2019, Brooks et al. 2020), the challenges of working with this exceedingly rare species present some important limitations to the current work. First, all of the drift fence data used to quantify flatwoods salamander phenology was collected relatively recently (2010–2020), especially when compared to other studies examining changes in amphibian phenology over time (Beebee 1995, Gibbs and Breisch 2001, Todd et al. 2011).
It is possible that the phenology we have observed in recent years has already shifted as a response to climate change, although immigration dates reported in the literature are relatively similar to the current study. Means et al. (1996) reported that 36 individuals were observed migrating to wetlands on October 9 (four days earlier than the earliest large movement reported here) and that all but one individual encountered on December 21 were moving away from breeding wetlands. Palis (1997) reported most movements into wetlands occurred from late

October to mid-December. Second, both populations included in the current study are small, and we used movements of just five individuals to quantify environmental conditions during large movement events. In many years, there were few movement events that met this threshold, making it challenging to draw strong conclusions about drivers of salamander phenology. Third, we based future predictions on hydrologic models (Chandler et al. *In prep*) and three GCM models, using hard cutoffs to forecast future conditions. All of these modeling techniques include substantial uncertainty that is difficult to meaningfully quantify when examining salamander phenology, and we suggest caution when interpreting our results at fine temporal scales. Finally, larval flatwoods salamanders are members of a complex aquatic community (Whiles et al. 2004; Chandler et al. 2015; Chandler et al. 2021), and other members of the community may also respond to environmental changes. Interspecific interactions are important for larval salamanders (Whiles et al. 2004) and changing phenologies could alter these community interactions (Durant et al. 2005; Revilla 2014), although other factors may also be important (e.g., density dependent processes; Anderson et al. 2017).

Flatwoods salamanders are perilously close to extinction, with a variety of factors contributing to the decline and rarity of the species (O'Donnell et al. 2017; Semlitsch et al. 2017). We suggest that changes in phenology are unlikely to threaten populations on their own (especially over timescales meaningful for current conservation efforts) but could add stress to an already tenuous relationship with wetland hydrology and breeding success. Previous research has indicated that hydrologic conditions during the late 1990s to early 2000s were worse (drier) than at any point over the previous 119 years (Chandler et al. 2016). As suggested by our drift fence data, current conditions in some populations are likely unsuitable for species persistence, even without additional climate stressors (Brooks 2020). Other effects of climate change (e.g., sea level rise and large storm events; Walls et al. 2019) also represent more direct challenges to managing many flatwoods salamander populations than shifts in phenology. It is important to consider that individual populations may respond differently to combinations of altered phenology and other stressors. Successful conservation and management of flatwoods salamander populations will require site-specific management decisions that are based on the best available data for each population or metapopulation (requiring some type of long-term monitoring). Direct management of flatwoods salamander populations will continue to be mostly limited to actions taken during the breeding period (e.g., habitat improvements or hydrologic manipulations) until additional research identifies links between adult survival and environmental drivers. Future work must focus on ensuring that reproduction is occurring frequently enough to maintain population viability as well as supporting adult survival outside of the breeding season to bridge the gap between years with reproductive failure.

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Table 1. Adult Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) were captured immigrating into two wetlands across 10 breeding seasons (2010–2020) at drift fences on Eglin Air Force Base, Florida. Individuals were all uniquely marked, and we defined large movements as periods when ≥ 5 salamanders were captured either on a single dry day or over the course of a precipitation event (i.e., consecutive days of precipitation). The number of precipitation events indicates how many precipitation events occurred between the beginning of the breeding season and the last large movement. *The drift fence in Season 1 at Pond 5 was opened late and likely missed the largest movement of salamanders into the breeding wetland.

	Number of individuals	Number of large movements	Date range of large movements	Minimum daily temperature range on days with large movement (°C)	Number of precipitation events	Date by which 90% of immigration had occurred	Number of precipitation events for 90% immigration
Pond 4							
S1	82	4	11-02–12-31	6.5–17.5	6	12-31	6
S2	83	6	11-03–12-20	7.7–18.0	8	01-10	9
S3	33	3	11-26–12-16	5.3–12.3	6	01-09	7
S4	26	2	10-17–11-25	6.1–16.9	5	11-25	5
S5	101	4	10-13–11-22	10.3–18.8	4	12-06	5
S6	93	3	10-13–10-31	15.2–20.6	2	10-31	2
S7	43	4	11-08–12-04	11.0–15.7	4	12-07	5
S8	38	1	10-22	20.9	1	11-17	4
S9	56	4	10-17–11-05	10.5–18.2	3	11-05	3
S10	31	2	10-14–11-07	8.7–15.7	2	11-11	2
Pond 5							
S1*	13	1	12-31	6.6	6	01-04	6
S2	40	3	11-09–12-19	8.8–11.9	8	01-17	10
S3	20	1	12-07	12.2	5	01-14	7
S4	10	0	-	-	-	11-25	5

S5	71	4	10-28–12-27	8.1–15.9	7	12-27	7
S6	37	2	10-25–10-31	18.2–20.6	2	11-11	3
S7	20	2	11-30–12-04	15.4–15.6	5	12-11	6
S8	22	2	10-22–10-27	9.6–20.8	2	11-08	3
S9	24	1	10-17–10-23	16.3	1	11-05	3
S10	10	1	10-24	15.8	1	12-08	5

Table 2. Characteristics of Reticulated Flatwoods Salamander (*Ambystoma bishopi*) metamorph emigrations from two breeding wetlands on Eglin Air Force Base, Florida. Metamorphs were captured using drift fences and represent the only documented reproduction in these two breeding wetlands over 10 breeding seasons (2010–2020).

Year	Number of metamorphs	Number of days with metamorphs	Number of large movements	Date of earliest emigration	Date of latest emigration
Pond 4					
2014	149	27	9	2014-04-12	2014-05-20
2016	97	23	8	2016-03-24	2016-05-13
2017	210	32	9	2017-03-30	2017-05-21
2019	3	3	-	2019-03-31	2019-04-05
2020	1	1	-	2020-03-31	-
Pond 5					
2014	54	21	4	2014-04-14	2014-05-30
2016	54	19	5	2016-03-31	2016-05-22
2017	7	6	0	2017-04-05	2017-05-21
2019	1	1	-	2019-04-08	-

Table 3. Model results for linear regressions predicting dates of movement opportunities for Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) across 70 breeding seasons from 2030–2099. Movement opportunities are defined as periods of precipitation with mean temperatures ranging from 5.325–20.85°C.

Climate Scenario	Movement Opportunity	F	P	Beta	SE	R^2
HadGEM2-CC RCP 4.5	1st	1.04	0.31	-0.04	0.04	0.02
HadGEM2-CC RCP 4.5	4th	0.44	0.51	-0.06	0.08	0.007
HadGEM2-CC RCP 8.5	1st	20.38	<0.001	0.26	0.06	0.23
HadGEM2-CC RCP 8.5	4th	16.30	<0.001	0.36	0.09	0.21
HadGEM2-ES RCP 4.5	1st	2.32	0.13	0.05	0.03	0.03
HadGEM2-ES RCP 4.5	4th	0.83	0.37	0.07	0.08	0.01
HadGEM2-ES RCP 8.5	1st	30.11	<0.001	0.26	0.05	0.31
HadGEM2-ES RCP 8.5	4th	10.17	0.002	0.27	0.09	0.14
CCSM4 RCP 4.5	1st	2.64	0.11	-0.07	0.04	0.04
CCSM4 RCP 4.5	4th	2.69	0.11	-0.13	0.08	0.04
CCSM4 RCP 8.5	1st	0.71	0.40	0.03	0.04	0.01
CCSM4 RCP 8.5	4th	1.58	0.21	0.09	0.07	0.02

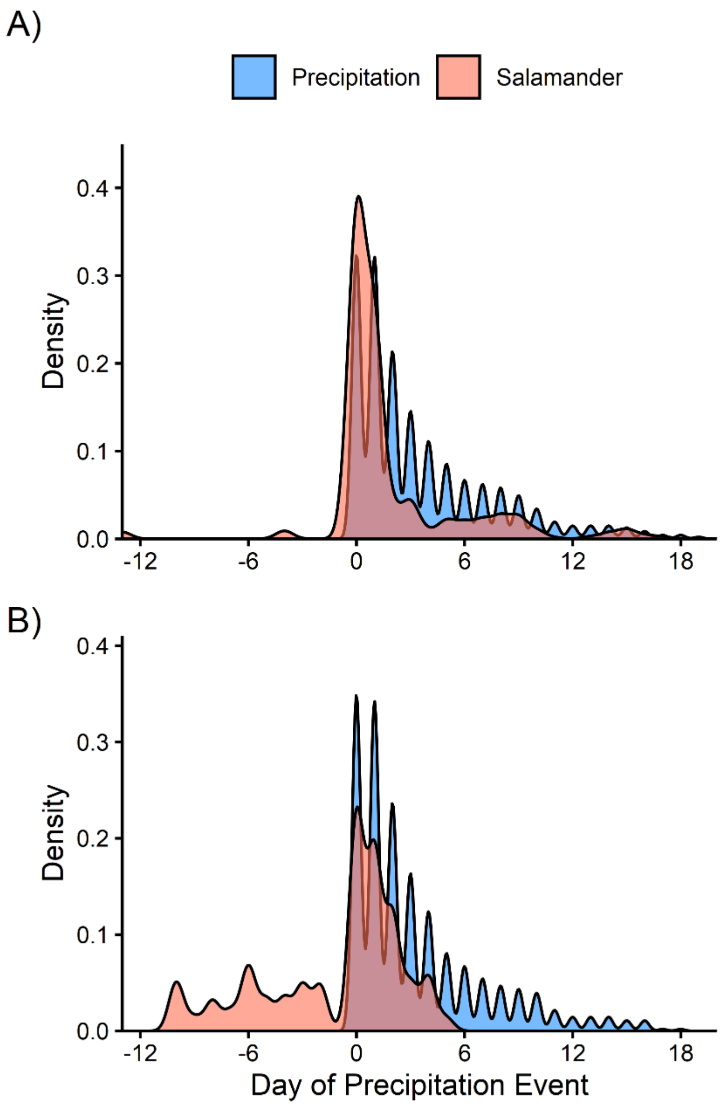

Figure 1. A) Adult Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) immigrating into wetlands and B) metamorphs emigrating out of wetlands were captured at two wetlands on Eglin Air Force Base, Florida from 2010–2020. Salamander movements are plotted with precipitation events, defined as periods of rain separated by at least three consecutive dry days. Day 0 represents the day before precipitation began, and negative values are dry periods between precipitation events. Captures were only included if at least five individuals were captured on a single dry day or across a single precipitation event.

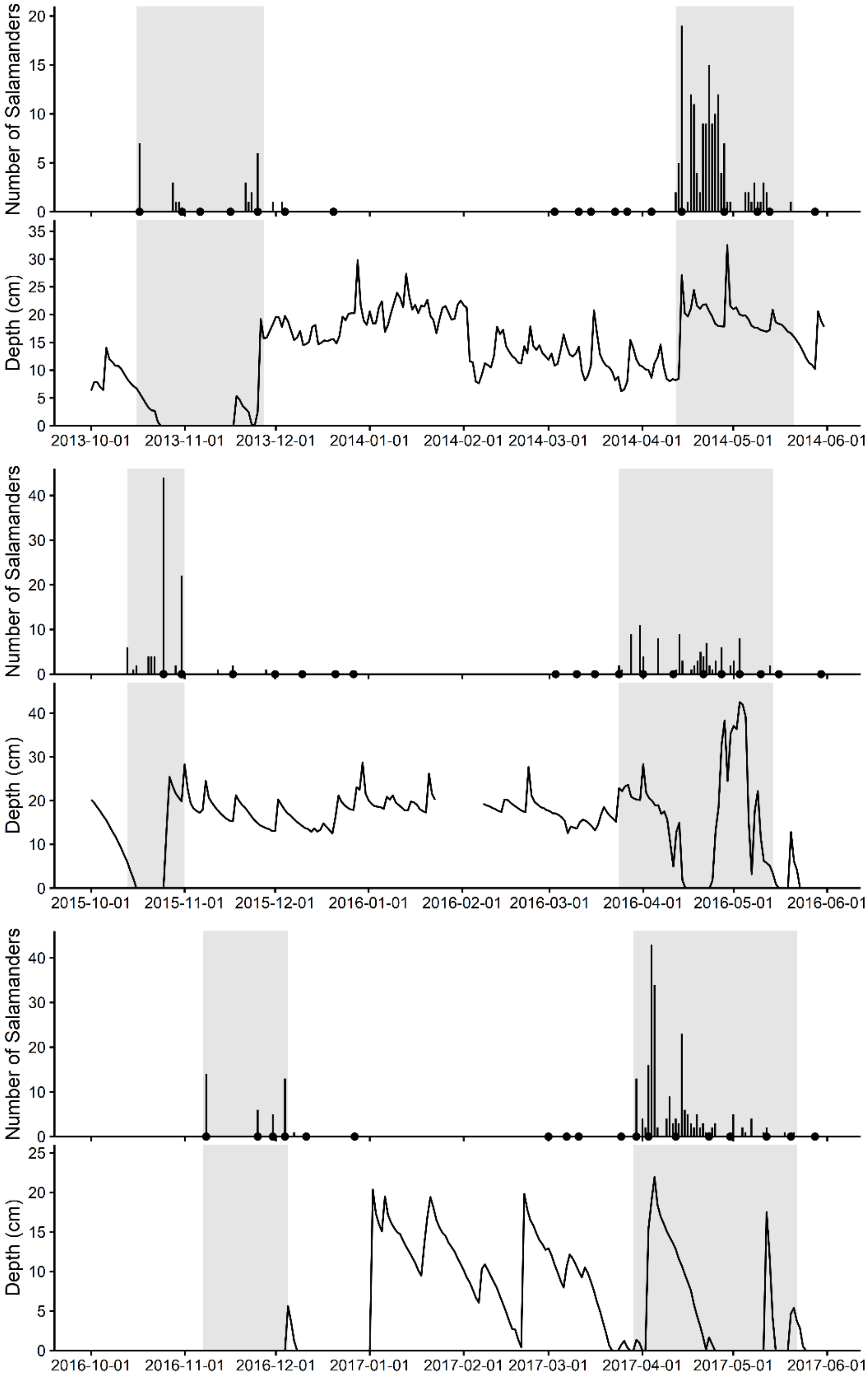

Figure 2. Characteristics of successful Reticulated Flatwoods Salamander (*Ambystoma bishopi*) breeding seasons from a breeding site on Eglin Air Force Base, Florida. Salamanders were

monitored using a drift fence over 10 breeding seasons (2010–2020), and only three of those seasons saw mass emigration of metamorphs during the spring. Shaded areas and bars on the left represent adult immigration, while shaded areas and bars on the right represent metamorph emigration. Black dots represent the beginning of precipitation events with temperatures conducive to salamander movements that occurred from October 13 through December 31.

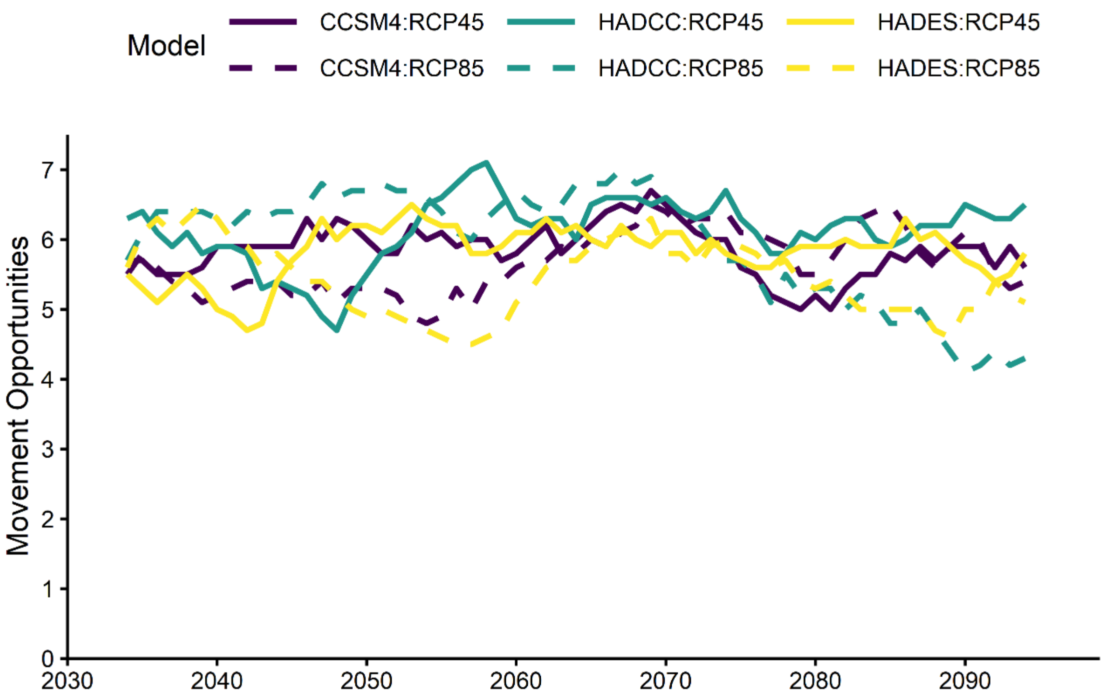

Figure 3. Potential movement opportunities for Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) were assessed under three climate models and two emission scenarios (RCP 4.5 and 8.5). Movement opportunities were defined as precipitation events with mean daily minimum temperatures between 5.325 and 20.85°C. The potential movement period was constrained to October 13 through December 31 of each breeding season. Lines represent 10-year moving averages.

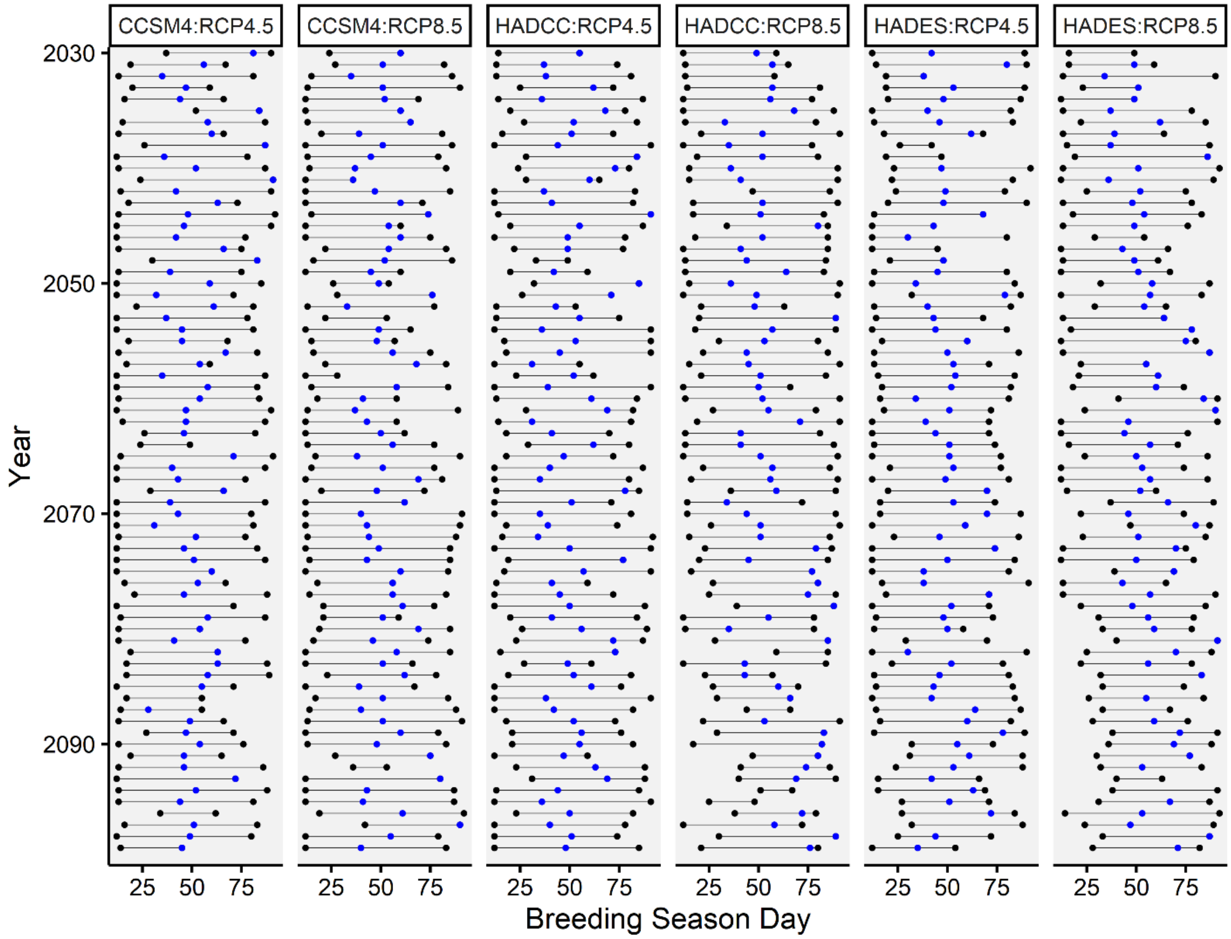

Figure 4. Predicted movement opportunities for Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) at breeding wetlands on Eglin Air Force Base from 2030–2099. A movement opportunity is defined as a precipitation event with mean minimum temperatures between 5.325 and 20.85°C that occurs from October 13 through December 31. These values are based on observed phenological variation. Black dots represent the 1st and last movement opportunity, while blue dots represent the 4th movement opportunity.

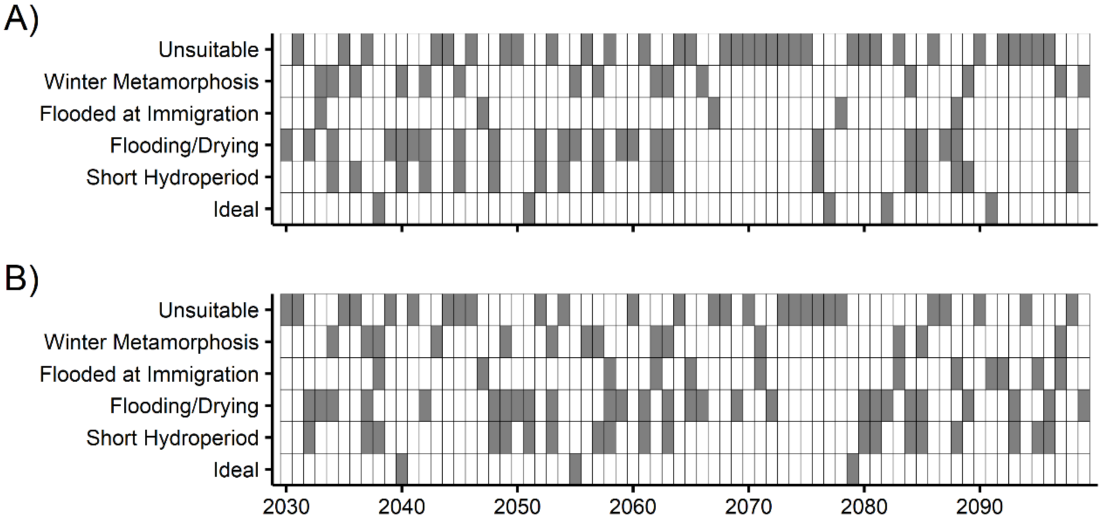

Figure 5. Examples of predicted conditions during future Reticulated Flatwoods Salamander (*Ambystoma bishopi*) breeding seasons for a single breeding site. Categories of breeding outcomes are defined under Methods, Data Analysis (p. 73). These predictions were based on the CCSM4 global circulation model and two representative concentration pathways (RCPs): (A) peak carbon emissions by 2040 (RCP 4.5) and (B) carbon emissions continue to increase through 2100 (RCP 8.5).

CHAPTER 3

Predicting long-term population viability for an imperiled salamander under future climate changes

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Abstract

Amphibians that breed in ephemeral wetlands typically exhibit cyclical dynamics whereby relatively high adult survival allows populations to persist through episodes of boom-and-bust recruitment. However, global changes that alter the normal cycle of events (e.g., the frequency of reproduction) can threaten the viability of these populations and limit the effectiveness of long-term management programs. We developed a stochastic Integral Projection Model for the Reticulated Flatwoods Salamander (*Ambystoma bishopi*) using demographic functions derived from 10 years (2010–2020) of drift fence monitoring on Eglin Air Force Base in the Florida Panhandle. We used this model to examine the responses of two salamander populations (occupying two breeding ponds; Ponds 4 and 5) to climate change by incorporating projections from three Global Circulation Models under two representative concentration pathways (emission scenarios; RCP 4.5 and 8.5). Using just wetland hydroperiod as a metric of reproductive success in future years, 16.7% (Pond 4) and 33.3% (Pond 5) of climate scenarios indicated a high probability of local extinction in the two wetland sites by the year 2100 (>50% chance). When accounting for potential interactions between salamander phenology and wetland hydrology that can reduce breeding success, the number of climate scenarios predicted to have a high extinction probability increased to 50.0% (Pond 4) and 67.7% (Pond 5) across the two salamander populations. Regardless of the modeling scenario, both complete and partial reproductive failure were common, highlighting the importance of maintaining high adult flatwoods salamander survival as a key management goal. Overall, our results indicate that there is a reasonably high probability that these two small flatwoods salamander populations will go extinct by the end of the century, mostly driven by severe droughts and repeated reproductive failure. Conservation and management actions should focus on maintaining high adult survival,

managing habitat to extend wetland hydroperiod, and promoting clusters of high-quality breeding wetlands that can undergo natural extinction and re-colonization dynamics, especially when larger, longer hydroperiod wetlands are closely associated with multiple small wetlands.

Introduction

Creating models to better understand and explain the dynamics of wild populations has been a major theme in ecology for many years (Lotka 1925; Volterra 1926; Wangersky 1978). Today, advances in statistical techniques allow researchers to fit complex models that account for many sources of biological, environmental, and individual-level variation (e.g., Duarte et al. 2017; Rice et al. 2018; Plard et al. 2019). Descriptive population models can be extended to apply directly to conservation and management programs for imperiled species, potentially explaining the processes that ultimately cause population declines or extinctions (Lande 1993; Caughley 1994). For example, population viability analyses (PVA) predict the likelihood that a population will persist over some period (Boyce 1992; White 2000), and PVA results have been used to directly inform management strategies for some species (e.g., Beissinger and Westphal 1998; Folt et al. 2019). However, PVAs have been criticized for using sparse datasets to build complex models and assuming that future conditions will be similar to current conditions (Coulson et al. 2001; Reed et al. 2002). To address potential issues, PVAs can leverage available data to accurately describe the population dynamics of the species in question, incorporate relevant environmental heterogeneity into the modeling framework, accurately predict (if projections are available) how these processes will change in the future, and be transparent about assumptions and uncertainty in the modeling process (White 2000).

Complex life cycles are a common amphibian adaptation, allowing species to take advantage of both aquatic and terrestrial environments (Wilbur 1980). It can be challenging to effectively quantify the population dynamics for such species as vital rates across life stages may be impacted by different biotic or abiotic factors. Furthermore, the population dynamics of species with complex life cycles can be complicated by a frequent reliance on ephemerally flooded conditions in wetland systems for reproduction and larval development (Cayuela et al. 2012; Taylor et al. 2005). Species that breed in ephemeral wetlands face a tradeoff of reduced predation pressure from a lack of established fish populations but a risk of complete reproductive failure in years where wetland hydrology is unsuitable (Skelly 1997). This uncertainty in reproductive success can cause large fluctuations in population size (Pechmann and Wilbur 1994; Taylor et al. 2005), and variable hydrologic conditions can impact larval growth rates and body size at metamorphosis (Pearman 1993; Brooks et al. 2020). Uncertainty in reproductive success is compensated for in many species with relatively high adult survival that allows populations to persist through drought years (Biek et al. 2002; Griffiths et al. 2010; Kissel et al. 2020). Overall, the challenges associated with modeling the population dynamics of amphibians have led many studies to focus on single vital rates or individual level effects rather than conducting a complete demographic assessment or viability analysis (Kiesecker et al. 2001; Biek et al. 2002; Vonesh and De la Cruz 2002, Schmidt et al. 2005).

Climate change has been linked to well-documented global amphibian declines for several decades (Pounds and Crump 1994; Carey and Alexander 2003). Amphibian physiology and life history characteristics make many species broadly susceptible to a variety of direct and indirect effects of climate change, including altered growth rates and body sizes, changes in behavior and phenology, long-term effects on habitat characteristics, and altered reproductive success (Blaustein et al. 2010; Todd et al. 2011; Li et al. 2013; Walls et al. 2013a). For example, research across multiple taxa has shown the potential negative effects of increased drought frequency on amphibian populations (McMenamin et al. 2008; Cayuela et al. 2016a; Bucciarelli et al. 2020). Synergistic effects between climate change and other environmental stressors can also exacerbate responses to climate change or interact in nonadditive ways to create complex conservation and management challenges (Pounds 2001; Rohr and Palmer 2013; Nowakowski et al. 2016). For imperiled species, quantifying the potential effects of climate changes on population dynamics and estimating extinction probabilities can provide useful metrics when considering a suite of potential management actions.

Reticulated Flatwoods Salamanders (*Ambystoma bishopi*; hereafter, flatwoods salamanders) exemplify many of the challenges faced by imperiled amphibians breeding in ephemeral wetland systems. Flatwoods salamanders are endemic to pine flatwoods of the southeastern United States and rely on frequent fires to maintain vegetation characteristics (open canopy, limited duff accumulation, and thick herbaceous vegetation along the forest floor) important for multiple aspects of their life history (Sekerak et al. 1996; Gorman et al. 2009; Jones et al. 2012; Gorman et al. 2014). However, flatwoods salamanders have experienced severe population declines and range contractions because of historic habitat loss, long-term fire suppression, and shifts in fire season (Bishop and Haas 2005; O'Donnell et al. 2017). In addition to historic declines, recent population declines have been linked to frequent droughts causing repeated reproductive failure (Palis et al. 2006). Furthermore, research has indicated that wetland hydroperiods have been shorter, on average, in recent years when compared to historical norms (Chandler et al. 2016). Overall, there is significant concern that climate change could jeopardize the success of extensive management actions that have been pursued in recent years (USFWS 2020), but there are currently no studies examining the potential magnitude of future changes and their effects on population viability.

We constructed a demographic model for flatwoods salamanders using data from a long-term monitoring and research program on Eglin Air Force Base, Florida. We then estimated extinction probabilities for representative flatwoods salamander populations describing the potential future effects of climate change on breeding phenology and wetland hydrology. We modeled climate change effects using six scenarios that cover a range of potential future conditions based on different climate models and emission scenarios. Our goals were to 1) describe flatwoods salamander demography and identify important areas of uncertainty; 2) conduct sensitivity analyses to identify vital rates most important to maintaining stable populations; 3) estimate extinction probability under multiple climate change scenarios; and 4) use the model results to make management recommendations for flatwoods salamanders.

Materials and Methods

Study Sites

We studied two populations of flatwoods salamander on Eglin Air Force Base in Okaloosa County, Florida from 2010–2020 (10 breeding seasons). These two populations breed in two small pine flatwoods wetlands (Pond 4: 0.45 ha; Pond 5: 0.36 ha). We completely encircled each breeding wetland with an aluminum flashing drift fence and captured salamanders moving into and out of wetlands each breeding season. The dates that drift fences were operational changed through time in response to weather conditions and staff availability, but we generally attempted to open fences in time to capture the first movement of individuals in the fall (October–November). We typically ran fences into the spring only when metamorphosis was likely (identified through larval dipnet surveys conducted every January through April) due to suitable hydrologic conditions (Appendix B: Table S1). We measured snout–vent length (SVL) and marked all captured metamorph and adult salamanders using a combination of Visual Implant Elastomers and Passive Integrated Transponders tags. Additional details of drift fencing methodologies are described in Erwin et al. (2016).

In addition to salamander monitoring, we also instrumented both breeding sites with a monitoring well placed near the centroid of the wetland. We installed monitoring wells in 2012 and recorded pressure inside the well every 15 minutes using HOBO® U20 pressure transducers (Onset Computer Corporation, Bourne, MA). We converted pressure measurements to water levels (relative to ground surface), correcting for barometric pressure variation using a U20 logger placed in the well head space (see Chandler et al. 2017 for more details).

Population Model

We modeled the population dynamics of flatwoods salamanders using an Integral Projection Model (IPM). This modeling framework accounts for variation within a population based on some continuous individual trait (most commonly body size), instead of dividing individuals into multiple stages as is commonly done in matrix models (Easterling et al. 2000; Ellner et al. 2016). The model incorporates continuous relationships between the selected individual trait and key demographic parameters (e.g., survival and fecundity) and accounts for individual growth through time (Childs et al. 2003; Ellner et al. 2016). IPMs have recently been used in a variety of different conservation projects and now present a flexible methodology for examining a variety of different population level processes across many taxa (Schreiber and Ross 2016; Caruso et al. 2020; Lown et al. 2020).

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

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

where z is a measure of body size, s(z) is a function describing the probability of survival based on size, $G(z',z)$ is the probability that an individual grows from size z to z', $F(z',z)$ represents a function describing fecundity based on body size (includes the probability that females reproduce in a given year, the number of offspring produced, the probability that offspring survive until time t + 1, and the size distribution of the new recruits), and $n(z,t)$ is the size distribution of the population at time t. The equation is integrated from L (the lower size limit) to U (the upper size limit). This range includes all possible body sizes that individuals can achieve, either by growth or shrinkage.

We constructed a variety of IPMs, ranging from mostly deterministic to mostly stochastic. We used model results to examine: 1) the effects of various model parameters and assumptions, and 2) the long-term effects of climate change on flatwoods salamander population viability. For stochastic IPM scenarios (see below), we drew survival and growth parameter values from posterior distributions, while allowing other vital rates to vary randomly across model runs (Table 1). This process creates a unique model kernel for each time step in the projection (Ellner and Rees 2007).

Demographic Functions

We used mark-recapture data collected from drift fences to build several functions describing important aspects of flatwoods salamander demography. Some of this work has been published elsewhere, but we briefly describe important demographic functions here. First, we assessed growth of post-metamorphic salamanders using a von Bertalanffy growth model, while accounting for individual-level variation in parameters defining the growth function (Brooks et al. 2020). We modified the growth function by lowering the variance in growth once individuals reached the size asymptote to reduce the frequency of eviction from the IPM (Williams et al. 2012). In addition to a growth model, we created two functions describing observed differences in size at metamorphosis based on wetland hydroperiod (i.e., a short vs. long hydroperiod breeding year) to account for the effects of hydrologic variation on individual size (Brooks et al. 2020). Second, we assessed post-metamorphic survival as a function of body size (SVL) using a multi-state robust-design Cormack-Jolly-Seber model (Brooks, unpublished data). For example, an individual with an SVL of 65 mm had an annual survival probability of 0.764 at the 90th percentile and 0.717 at the 10th percentile. Third, we modeled female reproductive output (egg production) as a function of body size (SVL) using available data from the published literature (Anderson and Williamson 1976) and by counting eggs in preserved specimens from the The Georgia Southern University – Savannah Science Museum Herpetology Collection. We used a simple linear regression model to describe the relationship between female body size and number of eggs produced (Chandler, unpublished data). We report parameter estimates and their associated variability for all demographic functions in Table 1 and Figures 1 and 2. Equations are given in Appendix D: Table S1.

Modeling Scenarios

To examine the effects of different parameter values on population growth rate and extinction probability, we fit a set of models where certain parameters were held constant across model runs. First, we focused on the effects of different reproductive values on population growth rate, while holding survival constant at the median size-specific value. Specifically, we examined the percentage of female salamanders reproducing in each breeding season (100%, 75%, or 50%) and the probability of surviving from an egg to returning in the following year

(1%, 2%, 3%, 4%, or 5%). Second, we examined the effects of differences in post-metamorphic survival (10th, 50th, and 90th percentile) and the frequency of complete reproductive failure due to unsuitable hydrology (50% vs. 67%) on long-term population viability. Finally, we also examined the effects of carrying capacity (i.e., a proxy for wetland size and availability of suitable terrestrial habitat) on the length of time that populations could persist without successful reproduction. Little is known about this value in practice, including whether there are density dependent effects that occur in the larval or adult phase.

We modeled the effects of future climate changes on flatwoods salamander population viability using three Global Circulation Models (GCMs) each with two Representative Concentration Pathways (RCPs). We chose the following models for inclusion in this study: Hadley Centre Global Environment Model 2 Earth Systems (HadGEM2-ES), Hadley Centre Global Environment Model 2 Carbon Cycle (HadGEM2-CC), and the Community Climate System Model Version 4 (CCSM4). The two RCPs represented within each model were 4.5 (assumes peak carbon emissions occur in 2040; Thomson et al. 2011) and 8.5 (assumes carbon emissions continue to increase until 2100; Riahi et al. 2011). Each model was downscaled to 6 x 6 km grids using the Localized Constructed Analogs (LOCA) method (Pierce et al. 2014). The final dataset included the same climate values for both wetlands involved in demographic modeling because they were within a single 6-km grid cell.

We used these climate data and the water level monitoring data described above to predict breeding season suitability based on how climate and hydrologic conditions relate to salamander phenology in each breeding season from 2030–2099. This work is described in detail in Chandler et al. (*In prep*) and Chapter 2. Briefly, we estimated several hydrologic characteristics for each breeding season, including the date of filling, the date of drying, and the longest hydroperiod. We also predicted the timing of immigration and emigration based on climate cues that are conducive to salamander movements (e.g., Brooks et al. 2019). We incorporated these analyses into population models using the following methodology. First, we used the length of the longest hydroperiod in each breeding season to determine whether reproduction was possible (hydroperiod ≥ 77 days; Palis 1995). If so, we determined the size distribution of metamorphs based on the hydroperiod (77–104 days = small; ≥ 105 days = large). We also classified years with wetland drying that would force metamorphosis in the winter (i.e., before mid-March) as reproductive failure because this is well outside the observed natural variation (labeled as winter metamorphosis in tables and figures; see Chapter 2). Second, we identified breeding seasons when hydrology may negatively interact with salamander phenology to contribute to reduced breeding success (categories of breeding outcomes are fully defined in Chapter 2 on p. 73 under Methods, Data Analysis). This included years when wetlands were flooded during all immigration events (potentially stranding terrestrial eggs) and years when flooding and drying occurred prior to the longest hydroperiod (potentially causing larval mortality). For these scenarios, we made no attempt to estimate the magnitude of these negative effects based on predicted water levels and instead treated them as stochastic effects that reduced the proportion of eggs surviving by a random value drawn from a uniform distribution (0.2–1.0). Because of the uncertainty surrounding this metric, we constructed models that just considered the effects of hydroperiod and models that considered the effects of both hydroperiod and phenology. A flowchart describing the complete process (Chapters 2 and 3) is presented in Appendix B: Figure S1.

We fit all models as female only models with an initial population size of 50 individuals. We selected the initial population density across body sizes based on one of the 20 observed densities from our drift fence data (held constant for models examining parameter effects and randomly drawn for climate scenario modeling; Appendix D: Figure S1). We set a carrying capacity of 75 for all simulations based on observed population sizes for these sites. For all simulations, we calculated extinction probability as the number of populations that declined below a quasi-extinction threshold of five individuals across 1,000 replicate model runs. In all climate scenario models, we randomly selected a proportion of eggs surviving to return in the following year (1–5%) and assumed that 100% of females at reproductive size returned to the wetland to breed (Table 1). We conducted both elasticity and sensitivity analyses to examine the effects of changes in both the survival-growth and fecundity kernels (Easterling et al. 2000). All analyses were conducted in R (R Core Team 2021).

Results

Parameter Examination

We found that population growth rates (λ) during successful breeding years were almost always greater than one under a variety of manipulations to the fecundity kernel, while holding post-metamorphic survival constant at the median value (Figure 3). There was a noticeable positive effect of longer hydroperiod (implemented through metamorph size; Figure 1) on population growth rate in successful breeding years (Figure 3). Decreasing the proportion of breeding females had larger effects during years when a higher proportion of eggs reached metamorphosis (e.g., mean decline in λ at 5% recruitment = 19.2% and mean decline in λ at 1% recruitment = 11.7% in years with long hydroperiods; Figure 3). Furthermore, small increases in the proportion of eggs surviving through metamorphosis had large effects on population growth rate (e.g., increases in average λ ranging from 41–54% in long hydroperiod years).

As expected, the frequency of successful breeding seasons had strong effects on extinction rates through time (Figure 4). For example, at median survival rates, increasing the average frequency of reproductive failure from 50% to 67% raised the extinction probability from approximately 8% to 59% after 70 years. Comparatively, changes in extinction probabilities across a range of survival values were smaller because of low overall variability in the survival function (e.g., 10th percentile of adult survival = 16% extinction probability vs. 90th percentile of adult survival = 4% extinction probability with a 50% chance for reproduction to occur; Figure 4). Even though the magnitude of change was smaller, we note that lowering post-metamorphic survival still resulted in a ≥4-fold increase in extinction probability. At median post-metamorphic survival, population size had a strong positive effect on the number of years that a population was likely to persist without successful reproduction (Figure 5).

Sensitivity and elasticity analyses for the fully stochastic kernel in years with long hydroperiods showed similar trends. Kernel level sensitivity indicated that changes to the kernel impacting the growth of juveniles into the reproductive size classes had the largest impacts on population growth rate (Appendix D: Figure S2A). Elasticity analyses indicated that survival and growth of individuals near the size at first reproduction had the largest impact on population growth rate, while changes to transitions of the most common sizes in the fecundity kernel had the biggest impact on population growth rate (Appendix D: Figure S2B–D). The results were similar in years with short hydroperiods but were generally shifted towards the smaller sized offspring in these years (Appendix D: Figure S3).

Climate Projections

We used the stochastic IPM to model flatwoods salamander population viability across six GCM-emission scenario combinations. Across all scenarios, population sizes fluctuated through time, experiencing relatively predictable declines during periods with hydrologic conditions that prevented reproduction and frequently reaching the carrying capacity during periods with frequent recruitment (Figure 6). Adding a penalty term for years in which hydrology and phenology may interact to reduce breeding success had strong negative effects on mean population size and increased the uncertainty in model projections (Figure 7). Overall, the model results indicated that flatwoods salamander populations at these two breeding sites had a high probability (>50%) of extinction in 16.7% (Pond 4) and 33.3% (Pond 5) of scenarios when just considering hydroperiod and 50% (Pond 4) and 66.7% (Pond 5) of scenarios when considering hydroperiod and phenology (Figure 8). Most other scenarios examined predicted extinction probabilities near zero.

Discussion

We combined a 10-year demographic dataset with site-specific hydrological and phenological projections made under multiple climate change scenarios to build an IPM for flatwoods salamanders and assess extinction probability over a 70-year period. Using only hydroperiod as a metric of breeding quality, predicted extinction probability exceeded 50% for only one and two of six potential climate scenarios at each breeding site, respectively. However, including the potential negative interactions between hydrology and phenology increased the number of scenarios with extinction probability above 50% to three and four out of six at each site. Accounting for interactions between hydrology and phenology is the most realistic modeling framework as the potential negative effects of intermittent hydroperiods and early flooding have been noted for both flatwoods salamanders (Palis et al. 2006; Gorman et al. 2014) and other ambystomatids (Semlitsch 1987; Jackson et al. 1989; Martin 1999). Thus, these small flatwoods salamander populations appear to face an approximately 50% chance of extinction by the end of the century under current management conditions.

We simulated flatwoods salamander population trajectories under a range of climate scenarios to capture the uncertainty inherent in these future projections. There were differences across models and emission scenarios, but variability among the three GCMs generally appeared to have larger effects on model results than differences between high and low emission scenarios (i.e., high emission scenarios were not necessarily worse than low emission scenarios for flatwoods salamanders). This variability among climate models is indicative of the high uncertainty in future projections of precipitation changes in the southeastern U.S., with projections ranging from relatively small decreases to large increases in precipitation by the end of the century (Anandhi and Bentley 2018). There is less uncertainty surrounding projections that overall evapotranspiration rates will increase, especially during the summer months (Seager et al. 2009). Ultimately, flatwoods salamander breeding wetland hydrology is likely to be impacted by changes to either precipitation or evapotranspiration rates (Sun et al. 2002; Chandler et al. 2017), but the magnitude of these changes is challenging to identify (Chandler et al. *In prep*).

Several modeling scenarios that predicted a high likelihood of extinction were characterized by long periods of frequent recruitment failure that almost always led to population crashes regardless of other stochastic factors (e.g., the CCSM4 RCP4.5 scenario). These types of long, severe droughts have been repeatedly highlighted as a potential threat to amphibian populations in the southeastern U.S. (Palis et al. 2006; Westervelt et al. 2013; Greenberg et al. 2015; Crawford et al. 2022), and even large populations are unlikely to persist through periods of low reproductive success that approach the adult lifespan. The challenges of meaningfully addressing prolonged droughts for a species like flatwoods salamanders are twofold. First, extensive monitoring data describing wetland hydrology, reproductive success, and population size are needed to identify thresholds for when additional management should be undertaken. Second, even if stakeholders decide that additional management is needed, there is no consensus about what those management actions should be. For flatwoods salamanders, additional management could range from artificially rearing salamanders to augmenting wetland hydrology (USFWS 2020; Seigel et al. 2006). Planning for these types of severe drought events is a critical management need because frequent reproductive failure over many years has a high likelihood to cause extirpations regardless of the habitat quality (i.e., even in well-managed landscapes).

Across all model parameterizations and climate scenarios, IPM results generally displayed fluctuating population sizes that are characteristic of amphibian species breeding in temporally dynamic ephemeral wetland systems (Green 2003; Taylor et al. 2005; Crawford et al. 2022). Even though there was substantial variability in potential parameterization of the fecundity kernel, population growth rates during successful breeding seasons were almost always greater than one and could approach two during exceptional years. Few successful breeding years were needed to rapidly increase population size from small to near the carrying capacity. High adult survival was uniformly important across all scenarios in allowing populations to persist through years with reproductive failure (Biek et al. 2002; Griffiths et al. 2010; Kissel et al. 2020). One important limitation to the current modeling framework is a limited mechanistic knowledge of the factors impacting adult survival, although previous research has indicated that survival does vary annually (Brooks 2020). Other research suggests that adult amphibian survival is likely linked to weather conditions experienced post-metamorphosis (Rittenhouse et al. 2009; Cayuela et al. 2016b). Thus, it is an important research need to understand the mechanisms impacting adult survival in flatwoods salamanders (e.g., the relationship between upland habitat quality and survival) and incorporate those relationships into future population viability models.

The IPM framework used here allowed us to quantify the potential effects of differing hydroperiods on body size at metamorphosis. Brooks et al. (2021) found that flatwoods salamander metamorphs were, on average, smaller during years with shorter hydroperiods than years with longer hydroperiods, and this trend has also been documented in other amphibian taxa (Scott 1990; Phillips et al. 2002). This difference in size at metamorphosis is important because individuals emerging as larger metamorphs are sometimes able to reproduce as yearlings in their first year returning to the breeding pond, while smaller metamorphs do not breed until at least their second year (Haas, unpublished data). Even if larger individuals do not breed until their second year, the larger size at first reproduction should contribute to an overall increase in lifetime fitness (Smith 1987; Semlitsch et al. 1988; Berven 1990). Other factors, including water temperature, the availability of prey, and the structure of the wetland habitat can also impact growth and size at metamorphosis in amphibians (Álvarez and Nicieza 2002; Skelly et al. 2002). Flatwoods salamanders are now regularly being raised in mesocosms as part of ongoing conservation work (USFWS 2020), and experimental studies examining the effects of the larval environment on growth and survival are now possible.

Despite 10 years of drift fence data, the current modeling framework was limited by key gaps in our basic natural history knowledge of flatwoods salamanders. First, we did not explicitly incorporate the approximately 5-month period between metamorphosis and the following breeding season. Post-metamorphic amphibians are generally considered to experience high predation and desiccation risk (Roznik and Johnson 2009; Burrow et al. 2021), but data describing this portion of the life cycle are lacking in flatwoods salamanders. It is likely that some of this early post-metamorphic mortality was captured in our egg survival parameter as some estimates of survival to metamorphosis exceed 5% (Shoop 1974; Petranka 1989). Second, we quantified the potential negative interactions between hydrology and phenology with a random draw from a uniform distribution. However, the magnitude of the effect on survival is highly dependent on a variety of factors (egg positions, water levels, wetland bathymetry, and larval ability to use underground retreats). Additional research is needed to better understand within-wetland responses to changes in phenology and hydrology. Third, there is considerable uncertainty in egg-laying behavior of female flatwoods salamanders, including the proportion of females breeding each season and whether eggs are always laid together or are sometimes dispersed (either spatially or temporally). These behaviors are likely to interact with hydrology to impact breeding success. Fourth, we did not account for either emigration or immigration of salamanders from one breeding site to another. While these processes are likely important at a landscape scale (Brooks et al. 2019), few observations of flatwoods salamanders moving between the two drift fenced wetlands have been recorded even though they are separated by just 250 m (Haas, unpublished data), making it challenging to meaningfully quantify these processes. Finally, we note that our modeling results are based entirely on data from small wetlands because of the logistical constraints of conducting high intensity population monitoring in large wetlands. Additional work is needed to better understand the effects of wetland or population size and surrounding upland habitat conditions on population viability. These assumptions and limitations of the current modeling framework provide a strong reminder that basic natural history and behavioral research are an important part of conservation programs.

Flatwoods salamanders have been driven to the edge of extinction because of widespread habitat loss, degradation, and poor wetland hydrologic conditions (Chandler et al. 2016; O'Donnell et al. 2017). The status of some remaining populations has been improved through widespread habitat improvements (Gorman et al. 2013; USFWS 2020), but uncertainty in long-term viability remains as climate change impacts the hydrology of ephemeral wetlands (Greenberg et al. 2015). Our IPM results suggest that these small flatwoods salamander populations have an approximately 50% chance of going extinct by the end of the century, driven primarily by repeated reproductive failure. This is somewhat unsurprising when considering the biology of amphibian populations breeding in ephemeral wetlands (e.g., Walls et al. 2013b). However, for flatwoods salamanders, it is concerning that populations that have experienced extensive management and conservation efforts are still at high risk of extirpation as a result of prolonged drought. We offer the following conservation and management recommendations for flatwoods salamanders when considering our model results. First, as is described in the species recovery plan (USFWS 2021), restoring clusters of three or more wetlands should be a priority to allow for regular extinction and colonization dynamics to occur. Second, larger wetlands that can support larger salamander populations are more likely to persist through periods of reproductive failure and should be a target of future restoration actions even if the restoration efforts needed are more intensive. Third, continued vegetation management, both within wetlands and in surrounding uplands (Jones et al. 2018), will have direct ecological benefits to salamander populations, improving hydrology and reducing stress from other factors.

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Table 1. Life history parameters that were modeled as part of a stochastic Integral Projection Model describing the population dynamics of Reticulated Flatwoods Salamanders (*Ambystoma bishopi*). Sources provided were used either in full or in part as justification for parameter values, and most parameters were directly estimated from 10 years of drift fence data monitoring two flatwoods salamander populations. Parameter values without citations were selected to improve model fit (e.g., reduce eviction of large individuals) or because of a lack of available data. See equations in Appendix D: Table S1.

Parameter Description	Values	Source(s)
Asymptotic size (mm) in von Bertalanffy growth model (L_∞)	70.0–77.9	Brooks et al. (2020)
Growth coefficient in von Bertalanffy growth model (k)	0.16–0.47	Brooks et al. (2020)
Deviation in growth for individuals < L_∞	3	Brooks et al. (2020)
Deviation in growth for individuals > L_∞	1	-
Mortality rate scale coefficient (μ)	0.74–1.31	Brooks (2020)
Mortality rate coefficient (β_1)	0.10–0.24	Brooks (2020)
Slope of the size-dependent fecundity function (m)	8.53	Chandler, unpublished data
Intercept of the size-dependent fecundity function (c)	-362.6	Chandler, unpublished data
Size at reproductive maturity (mm)	47.3	Chandler, unpublished data
Probability of recruitment from egg to metamorph, drawn from a uniform distribution	0.01–0.05	Brooks (2020); Shoop (1974); Petranka (1989); Stangel (1988)
Probability of female salamanders breeding	1.0	-
Mean metamorph size during long hydroperiod years, drawn from a uniform distribution	40.7–44.7	Brooks et al. (2020)
Deviation in metamorph size during long hydroperiod years	3.7	Brooks et al. (2020)
Mean metamorph size during short hydroperiod years, drawn from a uniform distribution	33.1–37.1	Brooks et al. (2020)
Deviation in metamorph size during short hydroperiod years	2.7	Brooks et al. (2020)

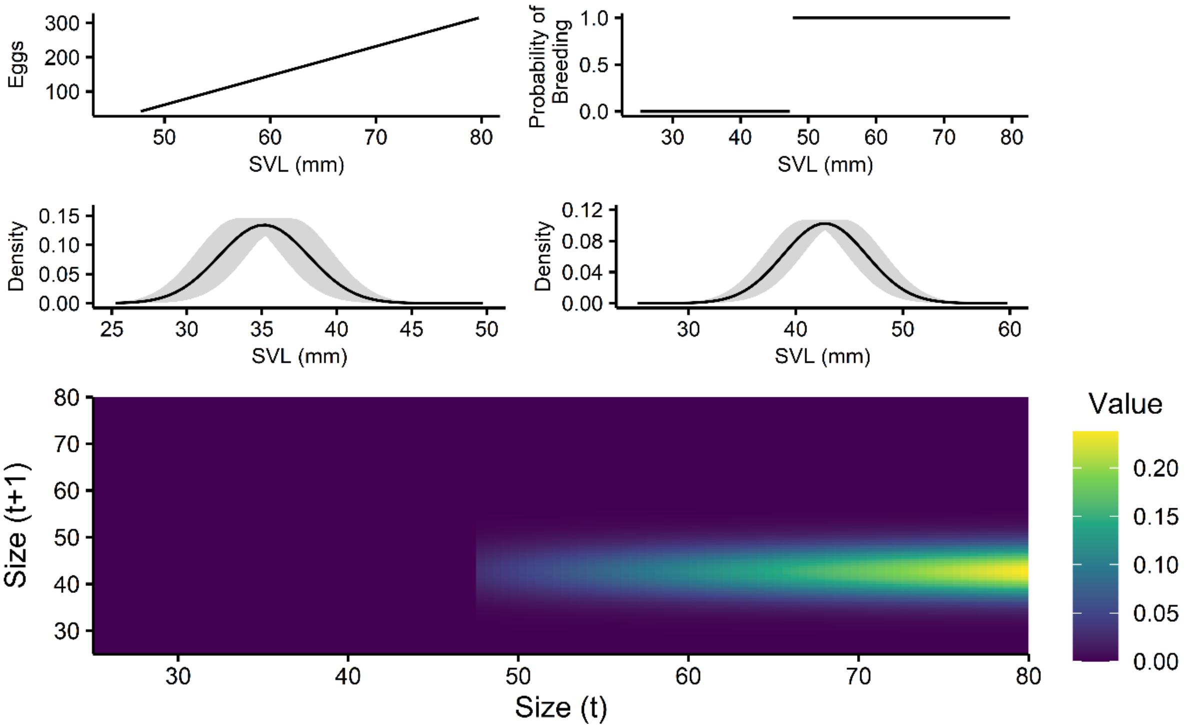

Figure 1. Demographic functions used to construct the fecundity kernel of an Integral Projection Model for Reticulated Flatwoods Salamanders (*Ambystoma bishopi*). Functions were mainly derived from monitoring data at two populations. Parameter values are provided in text and in Table 1.

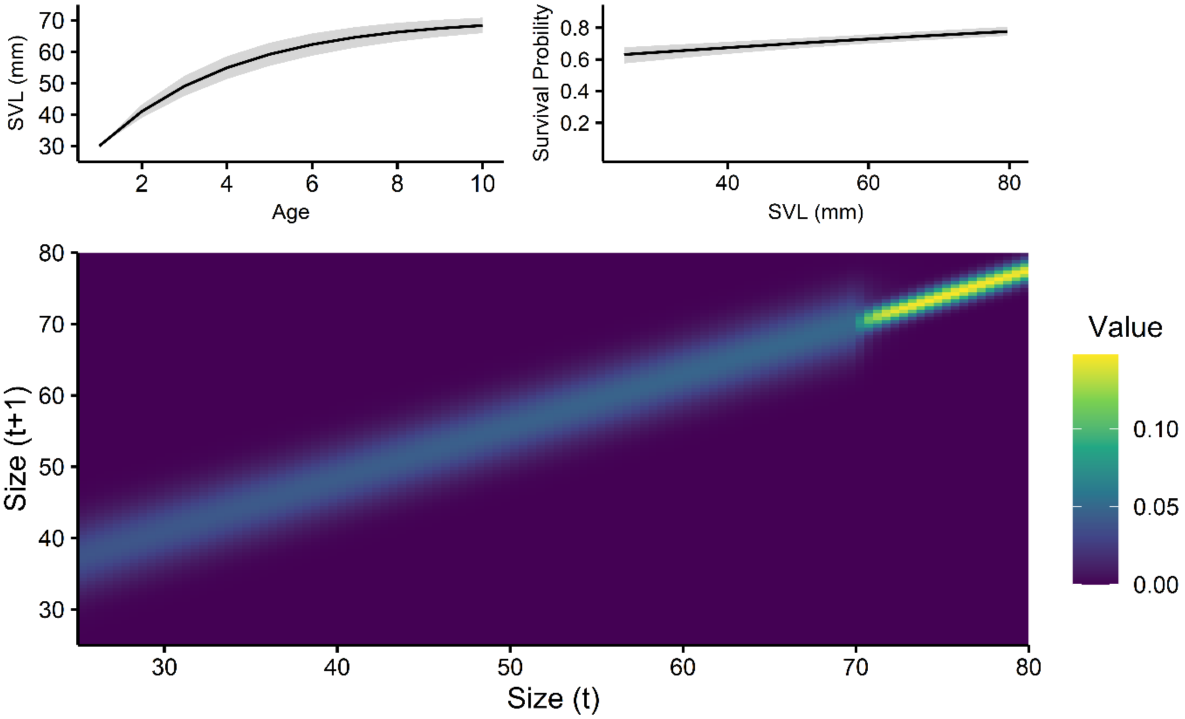

Figure 2. Demographic functions used to construct the combined growth and survival kernel of an Integral Projection Model for Reticulated Flatwoods Salamanders (*Ambystoma bishopi*). Functions were mainly derived from monitoring data at two populations. Parameter values are provided in text and in Table 1.

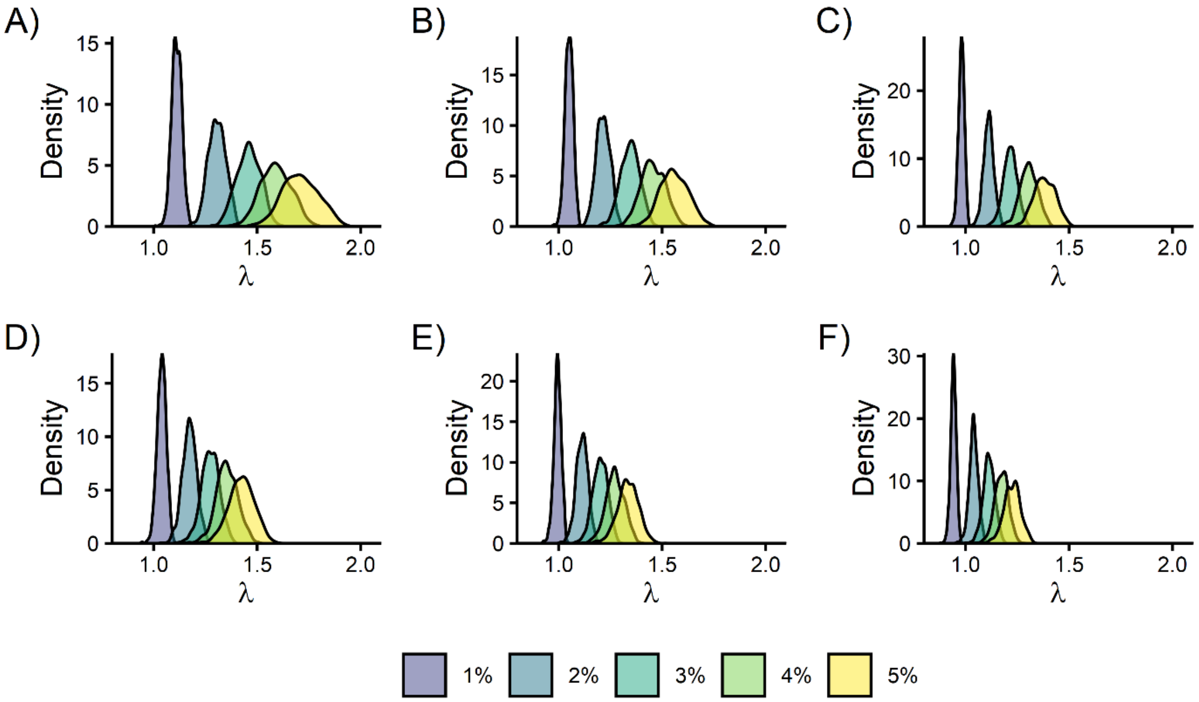

Figure 3. Population growth rates (λ) for various parameterizations of the fecundity kernel for an Integral Projection Model describing the population dynamics of Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) during successful breeding years. Fecundity kernels were parameterized with both large (A–C) or small (D–F) metamorph size distributions (mean size of large metamorphs = 40.7–44.7; mean size of small metamorphs = 33.1–37.1), reflecting differences in wetland conditions. The percentage of adult females returning to the wetland to breed ranged from 100% (A and D) to 75% (B and E) to 50% (C and F). Finally, the probability of individuals starting as eggs, surviving through metamorphosis, and returning to the wetland in following year was 1–5%. Post-metamorphic survival was held constant at the median value.

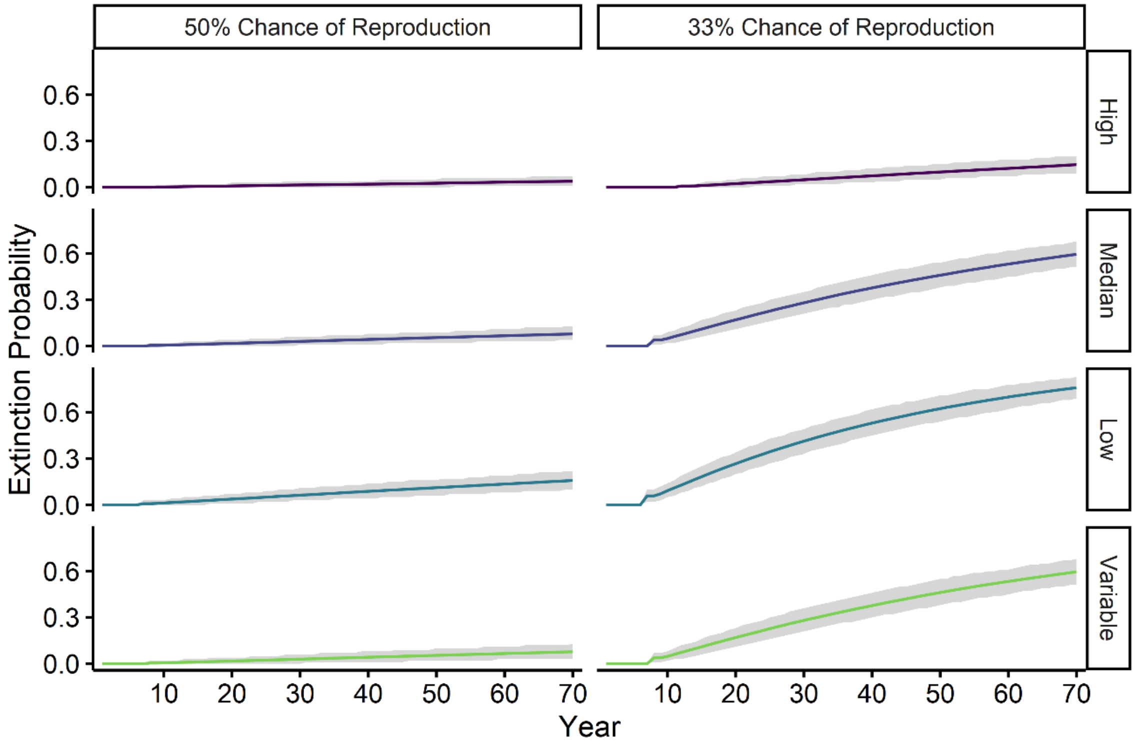

Figure 4. Extinction probabilities for Reticulated Flatwoods Salamander (*Ambystoma bishopi*) populations based on results of an Integral Projection Model. Probability of successful metamorphosis ranged from 50–33%, and post-metamorphic survival was held constant at the 90th (high), 50th (median), or 10th (low) percentile. Variable survival represents a random draw from the posterior distribution describing the survival function. Shaded regions equal 90th percentiles from replicate runs.

Figure 5. The relationship between population size and the number of years that a Reticulated Flatwoods Salamander (*Ambystoma bishopi*) population can likely persist without successful recruitment based on the results of an Integral Projection Model. The blue line represents the cubic fit to the raw data.

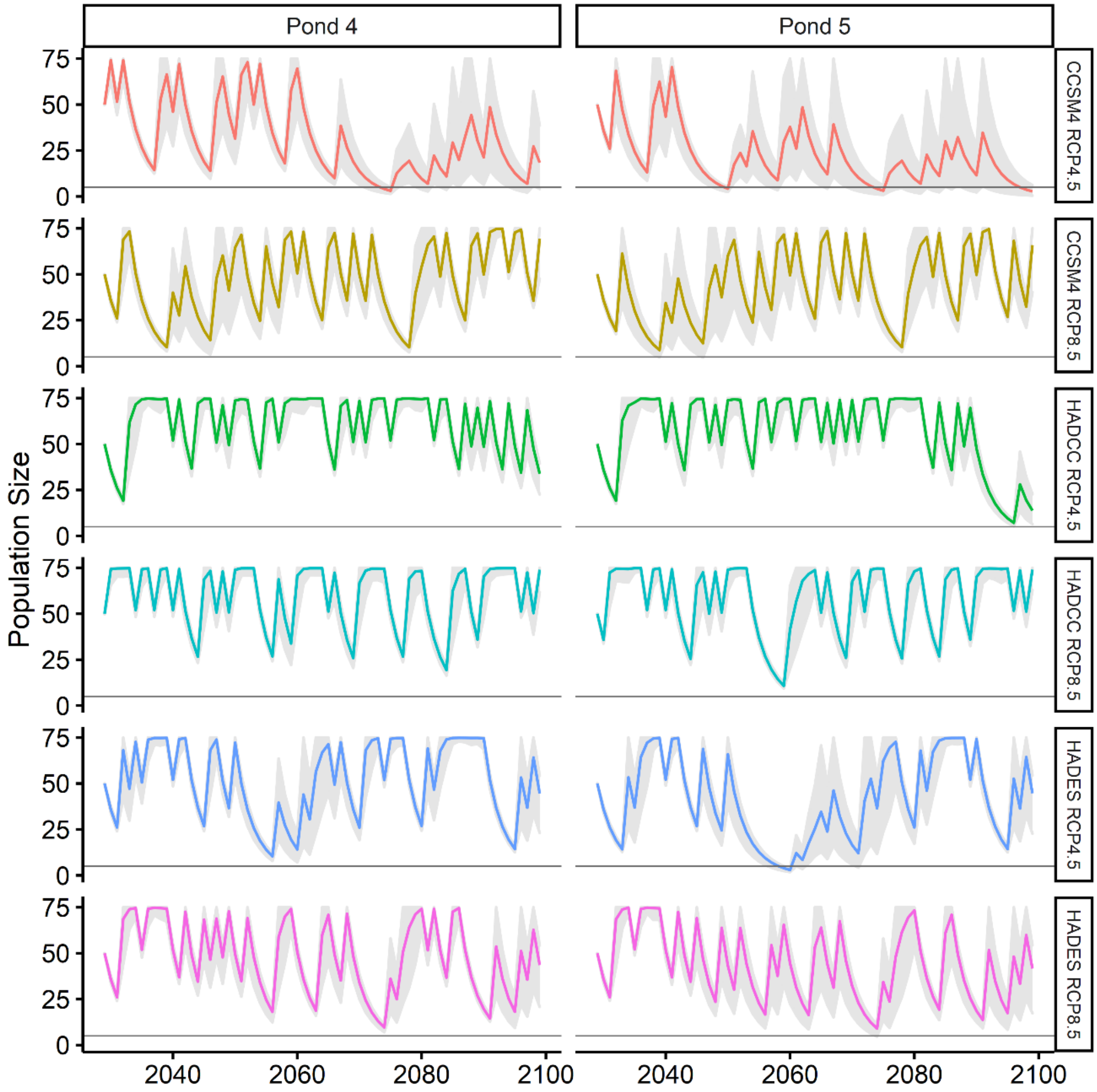

Figure 6. Projected Reticulated Flatwoods Salamander (*Ambystoma bishopi*) population sizes under six different Global Circulation Model and representative concentration pathways (emission scenario) combinations calculated for two ponds in the Florida panhandle. Results are based on a stochastic Integral Projection Model where predicted wetland hydroperiod was used to assess the quality of future breeding seasons, and carrying capacity was set at 75 females. Shaded regions represent 95th percentiles from replicate runs, and horizontal gray lines represent

a quasi-extinction threshold of five individuals. Note that scenarios were allowed to run for the entire period even if they crossed below the quasi-extinction threshold.

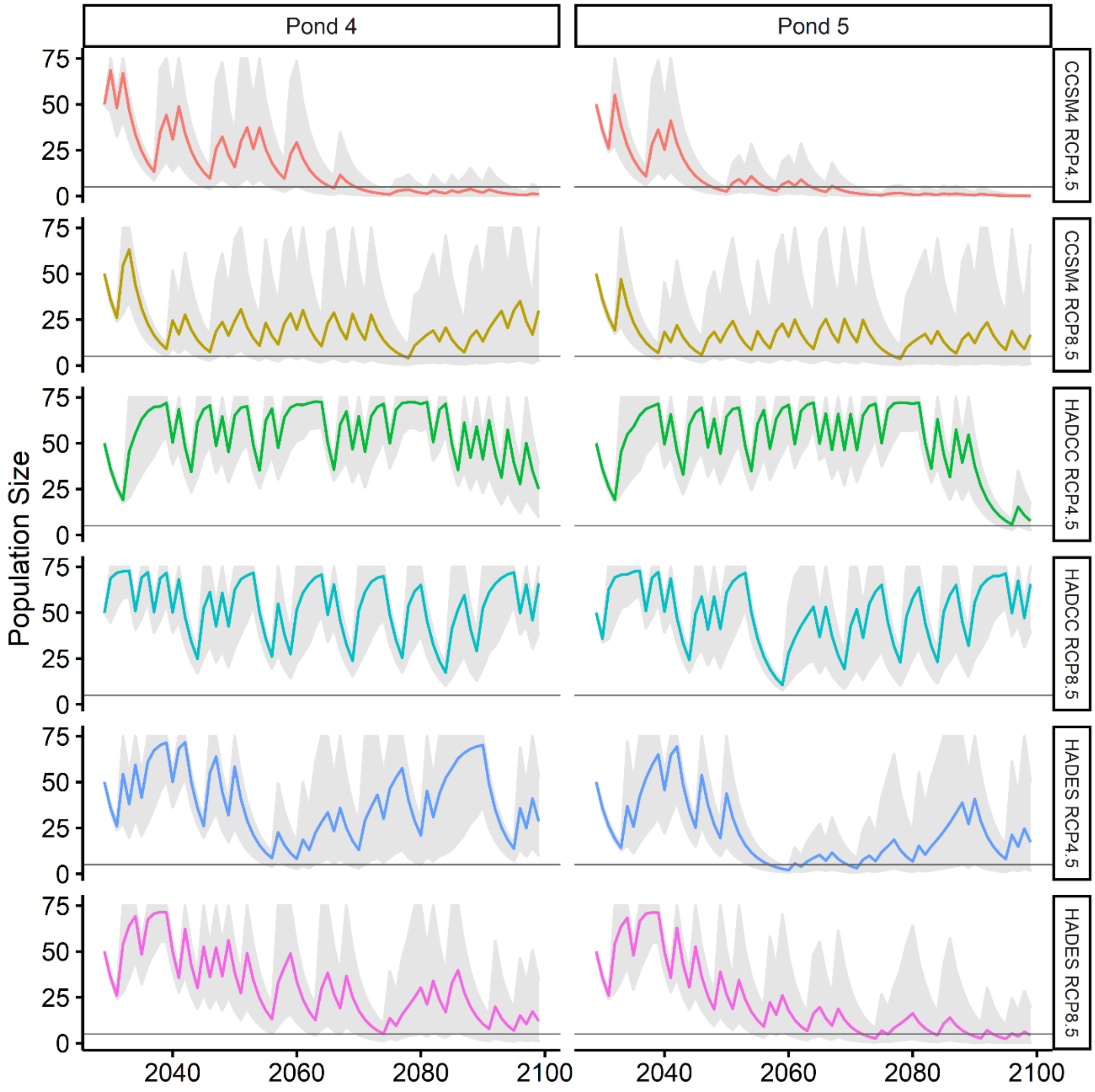

Figure 7. Projected Reticulated Flatwoods Salamander (*Ambystoma bishopi*) population sizes under six different Global Circulation Model and representative concentration pathways (emission scenario) combinations for two ponds in the Florida panhandle. Results are based on a stochastic Integral Projection Model where predicted wetland hydroperiod and potential interactions between hydrology and salamander phenology were used to assess the quality of future breeding seasons. Carrying capacity was set at 75 females. Shaded regions represent 95th percentiles from replicate runs, and horizontal gray lines represent a quasi-extinction threshold of

five individuals. Note that scenarios were allowed to run for the entire period even if they crossed below the quasi-extinction threshold.

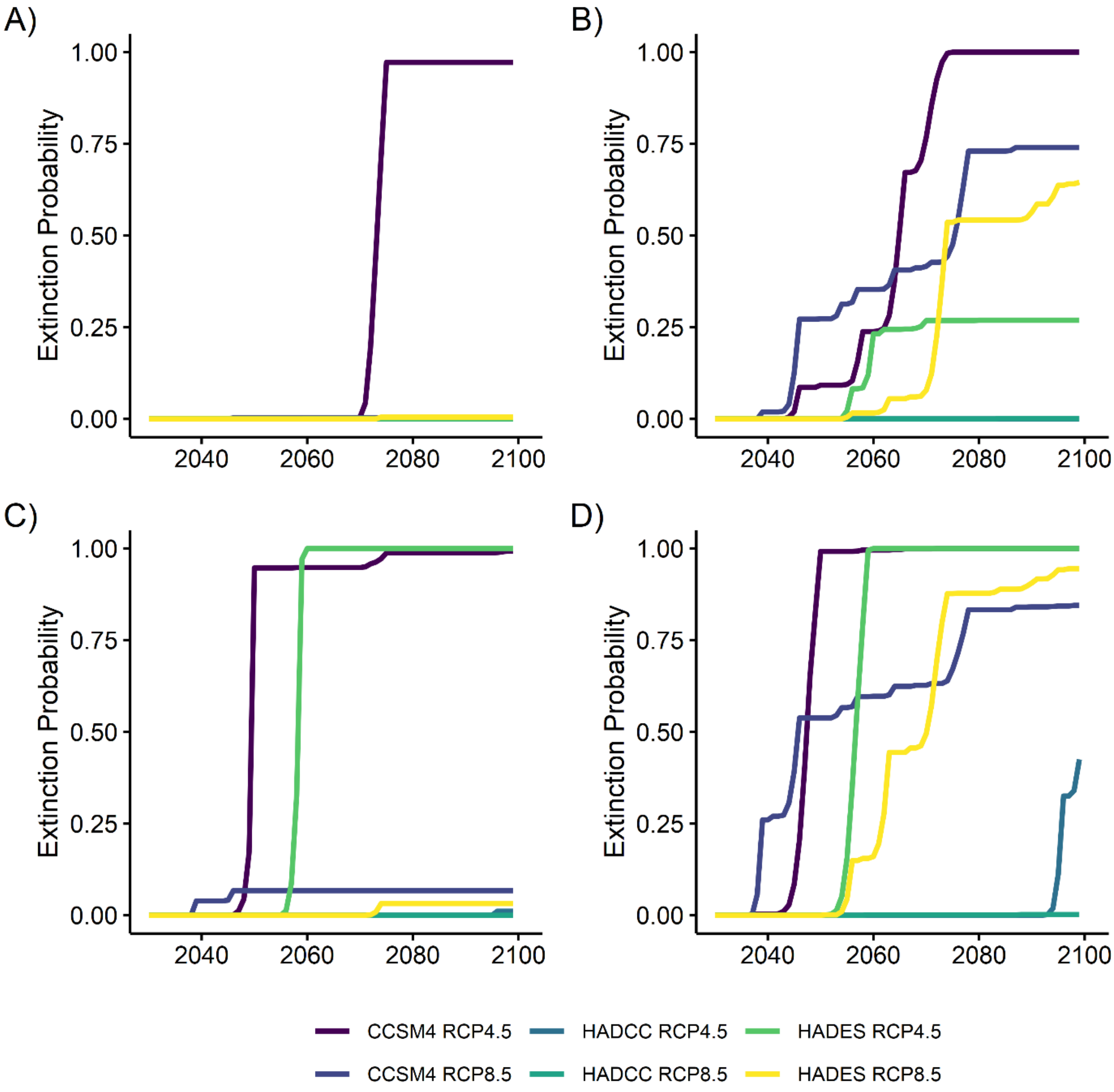

Figure 8. Extinction probabilities for two Reticulated Flatwoods Salamander (*Ambystoma bishopi*) populations (Pond 4: A and B; Pond 5: C and D) based on six different climate model and emission scenario (RCP 4.5 and 8.5) combinations. Both wetlands support relatively small flatwoods salamander populations in the Florida Panhandle. Results are based on a stochastic Integral Projection Model where the quality of future breeding seasons were quantified based just on projected hydroperiods (A and C) and then with hydroperiods and potential interactions

between salamander phenology and hydrology (B and D). Scenarios with lines not visible represent an extinction probability at or near zero.

CHAPTER 4

An integral projection model for the imperiled Eastern Indigo Snake (*Drymarchon couperi*)

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Abstract

Snake populations are frequently susceptible to the negative effects of habitat fragmentation, especially when habitat patches are bisected by dense road networks. However, snakes are often challenging to study, making a quantitative assessment of population responses to potential threats or management actions difficult. This can hamper conservation efforts for imperiled species by limiting the ability of wildlife agencies to meaningfully allocate limited resources. Here, we developed an Integral Projection Model for the imperiled Eastern Indigo Snake (*Drymarchon couperi*) using a variety of data sources. We used this model to assess population viability under a range of representative scenarios that focused on 1) road density, 2) initial population size, and 3) collection to support captive breeding efforts. We found that extinction probabilities were low across a range of road densities and initial population sizes but that, on average, the negative effects of high road densities on survival led to slow, sustained population declines (i.e., population growth rates just under one on average). The highest collection rates examined (four adults per year or two clutches per year) rapidly lead to high extinction probabilities, while dividing this effort among at least four populations reduced the extinction risk. The modeling results also indicated that collection of adult females had stronger negative effects on populations than collection of eggs. Indigo snake populations continue to face a variety of threats across their contemporary range, and understanding the effects of various threats or management actions on long-term population viability will be a key planning tool for future conservation efforts.

Introduction

Increasingly fragmented natural landscapes are a nearly ubiquitous characteristic of the human-dominated global environment (Haddad et al. 2015). Both the direct loss of habitat through conversion of natural systems to anthropogenic land uses and the breaking apart of habitat into isolated patches can negatively impact wildlife populations (Fahrig 2003). Patch size is often the most important characteristic determining the effects of fragmentation on populations (Keinath et al. 2016), but long-term negative effects of anthropogenic landscape characteristics (e.g., roads) can also threaten the viability of populations within otherwise suitable habitat patches (Ferreras et al. 2001). Thus, effective conservation planning, especially at broad spatial scales, requires an understanding of how landscape configuration interacts with potential threats or management actions to impact important demographic processes and ultimately population viability.

In the United States, the U.S. Fish and Wildlife Service is tasked with making decisions surrounding the listing and conservation of at-risk species under the Endangered Species Act (United States 1973). Currently, decisions are based in part on Species Status Assessments (SSAs) that use the best available science to determine the status, threats, and potential responses to future changes for species that have been petitioned for listing or are already listed (Smith et al. 2018). Population viability analyses (PVA) are increasingly included in SSAs, allowing stakeholders to better understand how populations may change through time as a response to a variety of threats (McGowan et al. 2017). However, PVAs have been criticized for building complex ecological models for species that are poorly studied or that possess cryptic life histories, such that limited demographic data are available to incorporate into a population model (Coulson et al. 2001; Reed et al. 2002). While these criticisms can be warranted and assumptions in the modeling process should be clearly identified and assessed, PVAs are often one of the best tools available when attempting to quantitatively assess a species' status and evaluate the likelihood of different outcomes, in order to allocate limited conservation resources to have the largest impact (Drechsler and Burgman 2004; McGowan et al. 2017).

Many snake species (Suborder Serpentes) are challenging to study because of clandestine life histories and generally low detection probabilities using standard survey techniques (Durso et al. 2011; Böhm et al. 2013; Dorcas and Wilson 2013). This can lead to sparse datasets that are difficult to analyze using a variety of statistical techniques, limiting the ability of researchers to estimate important demographic metrics (e.g., abundance; Steen 2010). A lack of robust datasets describing species' natural history, ecology, and population demographics limits the effectiveness of status assessments (i.e., many snake species are data deficient; Böhm et al. 2013; Bland and Böhm 2016) and the identification of stressors leading to suspected population declines (Winne et al. 2007). Furthermore, many existing data gaps are exacerbated by current limitations in technology and available survey methodologies (e.g., monitoring fossorial species; Wilson and Dorcas 2004). These limitations to understanding snake natural history and ecology are important because snakes often fill critical ecological roles, as both abundant community members (Fitch 1975) and top predators (Bestion et al. 2015). Given concern about widespread declines of snake populations (Reading et al. 2010), identifying creative ways to leverage existing data from a variety of sources to better understand demographic processes and inform management of imperiled snake fauna is a critical research need.

The Eastern Indigo Snake (*Drymarchon couperi*; hereafter, indigo snake) is the longest snake native to North America, with males occasionally reaching lengths exceeding 2.4 meters. Historically, indigo snakes were native to parts of southern Mississippi, Alabama, Georgia, and all of Florida. Today, populations have been extirpated from the western portion of their historic range (except for two reintroduced populations) and occur only in southern Georgia and peninsular Florida (USFWS 2019). Range contractions and evidence of population declines in other regions led the U.S. Fish and Wildlife Service to list indigo snakes as Threatened on the Endangered Species List in 1978 (USFWS 1978). This listing status largely removed some potential threats to indigo snake populations (e.g., collection for the pet trade) but other serious threats remain (e.g., habitat loss and fragmentation), resulting in continued listing of the species after the most recent SSA (USFWS 2019).

Compared to many other snake species, a large amount of research has been conducted on various aspects of indigo snake ecology, including movements, spatial ecology, survival rates, and disease prevalence (e.g., Breininger et al. 2004, 2012; Stevenson et al. 2009; Hyslop et al. 2009, 2012, 2014; Chandler et al. 2019; Bauder et al. 2020). In addition to these published studies, several unpublished datasets exist that can be used to inform indigo snake conservation projects (see below). However, there are currently no range-wide, quantitative assessments of indigo snake population viability. Existing assessments of indigo snake population dynamics examine site-specific management scenarios (Breininger et al. 2004; Folt et al. 2019) or rely heavily on detailed movement data (Bauder 2019). In the SSA, the U.S. FWS (2019) delineated population units and ranked them based on hypothesized future changes but did not assess viability using a population modeling approach. Thus, creating a flexible modeling framework that can be used to assess population viability across the species' distribution and under a variety of potential management scenarios or future threats would provide important information to benefit indigo snake conservation.

Here, we expand on previous population modeling efforts for indigo snakes by developing a stochastic Integral Projection Model (IPM) using available demographic data for this species. We present our model in a flexible framework that can be used to examine a variety of potential conservation and management scenarios for indigo snakes across their range. To demonstrate the model's utility, we examine two scenarios: 1) the effects of initial population size and surrounding landscape characteristics (i.e., road density) on long-term population viability, and 2) the effects of intentional collection (to support the captive breeding efforts) on wild indigo snake populations.

Materials and Methods

Indigo Snake Data

We collected data describing indigo snake demographic processes and population characteristics from various sources, including both the published literature and ongoing indigo snake conservation projects. First, morphometric and mark-recapture data have been collected from a number of sites across southeastern Georgia as part of long-term population monitoring projects (Stevenson et al. 2009; Bauder et al. 2017). Second, multiple radio telemetry projects documenting indigo snake survival in both Georgia and Florida have been completed in recent years (Breininger et al. 2011; Hyslop et al. 2012; Bauder et al. 2016). Third, a wide variety of data describing body size, growth, and reproductive output have been collected as part of ongoing captive breeding efforts to support reintroduction projects (e.g., Wines et al. 2015). We leveraged these available datasets to model several important demographic processes (see below). We also used the available data to create a range-wide habitat suitability model (Chandler et al. 2022) and delineated conservation units describing the spatial distribution and connectedness of indigo snake habitat across the species' distribution (Bauder et al. 2022). Both models were completed as initial phases of the current project and used to refine the spatial assessment of indigo snake populations originally produced by USFWS (2019).

Population Model

We combined the above datasets to model the population dynamics of indigo snakes using a stochastic IPM. Rather than dividing individuals into multiple stages (commonly done in matrix models), IPMs account for demographic variation within a population based on a continuous individual trait (e.g., body size; Easterling et al. 2000; Ellner et al. 2016). We allowed key demographic parameters (e.g., survival and fecundity) to vary across a range of indigo snake body sizes and accounted for individual growth through time (Childs et al. 2003; Ellner et al. 2016). For stochastic IPM scenarios, we drew survival and growth parameter values from posterior distributions of previous analyses, while allowing other vital rates to vary randomly across model runs (Table 1). This process creates a unique model kernel for each time step in the IPM projection (Ellner and Rees 2007).

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

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

where z is a measure of body size, s(z) is a function describing the probability of survival based on size, $G(z',z)$ is the probability that an individual grows from size z to z', $F(z',z)$ represents a function describing fecundity based on body size (includes the probability that females reproduce in a given year, the number of offspring produced, the probability that offspring survive until time t + 1, and the size distribution of the new recruits), and $n(z,t)$ is the size distribution of the population at time t. The equation is integrated from L (the lower size limit) to U (the upper size limit). This range includes all possible body sizes that indigo snakes can achieve, either by growth or shrinkage.

Demographic Functions

We used the above datasets to construct functions describing various aspects of indigo snake demography. For all analyses, we used snout–vent length (SVL) as our metric of body size. These analyses are described in detail elsewhere and are briefly discussed here. To model growth, we fit a von Bertalanffy growth model that accounted for both individual heterogeneity in growth and sex-specific differences (Chandler et al. *In review*). Furthermore, we described the potential size distribution of hatchling snakes using body size measurements recorded during captive breeding efforts (Table 1). To quantify the number of eggs produced by female snakes as a function of body size, we fit a linear regression model to data from both captive and wild snakes whose body size and clutch sizes were recorded (see Wines et al. 2015 for description of a similar model). Preliminary analysis suggested there were no significant differences between captive and wild snakes, so we combined the datasets to produce a single estimate for a linear relationship between female body size and clutch size (Table 1). Finally, we used a combined dataset of mark-recapture and radio telemetry data to estimate indigo snake survival as a function of both body size and anthropogenic landscape factors. We fit a Bayesian state-space model (Kery and Schaub 2012) and used road density, which has been previously shown to negatively impact indigo snake survival (Breininger et al. 2012), as our metric of anthropogenic impacts in the survival function (Bauder, unpublished data). As expected, we found a mostly negative relationship between road density and survival and a mostly positive relationship between body size and survival (both credible intervals slightly overlapped 0; Table 1). We report parameter estimates and their associated variability for all demographic functions in Table 1 and Figures 1 and 2. Equations are given in Appendix E: Table S1.

Modeling Scenarios

Prior to examining population viability, we evaluated the effects of different parameterizations of the fecundity kernel on population growth rate (λ). Little is known about indigo snake reproduction in the wild (but see Smith 1987; Stevenson et al. 2021), and this portion of the model had the most uncertainty associated with parameter values. We evaluated the combined effects of four hatching rates (40%, 50%, 60%, and 70%) and three proportions of females reproducing (following Folt et al. 2019) during the breeding season (100%, 85%, and 70%). For each combination of factors, we held survival constant at the median value but allowed other parts of the IPM to vary stochastically (i.e., the hatchling size and growth functions). We then assessed λ across 1,000 iterations of the kernel.

We fit a variety of models to examine the effects of various parameter values, landscape configurations, and management scenarios on representative indigo snake populations. We used the results of Chandler et al. (2022) and Bauder et al. (2022) to identify a high, medium, and low road density characteristic of the variability across delineated indigo snake populations (high = 0.045, medium = 0.017, and low = 0.005). We calculated all road density values using the Tiger Roads layer (US Census Bureau 2020). We also used the size of delineated units from Bauder et al. (2022) and existing home range estimates (Hyslop et al. 2014; Bauder et al. 2020) to identify a range of potential population sizes (15, 30, 60, and 120). These values were selected to be representative of the conditions that indigo snake populations may experience across their range in both Georgia and Florida. Some populations on large conservation lands (e.g., Fort Stewart) are likely much larger than those considered here, but our analyses were focused on relatively small populations that characterize most remaining indigo snake habitats.

We assessed all scenarios using the following framework. We modeled indigo snake populations using a female only model and assumed that all females of reproductive size (SVL ≥ 1.23 m) had access to male snakes. For each simulation, we set a carrying capacity that was equal to approximately 125% of the initial population size. We simulated indigo snake population trajectories over 100 years for each scenario and calculated extinction probability as the number of 100 replicates where the population declined below a quasi-extinction value of five individuals. We repeated this process 1,000 times to generate means and confidence intervals for extinction probabilities. No data are available describing the distribution of sizes in wild indigo snake populations, so we initiated simulations using a constant size distribution. We conducted both elasticity and sensitivity analyses using the mean kernel to examine the effects of changes in both the survival-growth and fecundity kernels (Easterling et al. 2000).

We also simulated the potential effects of collection from wild populations to support the captive breeding colony through two alternative methodologies. First, we examined the effects of removing adult females from the population at three different rates (four, two, and one female annually). Second, we modeled the effects of removing eggs from the population at three different rates (two or one clutch annually and one clutch every other year). Collection rates in all scenarios were based on a hypothetical maximum number of snakes needed to support the captive colony (Bogan, personal communication) and then splitting that effort across one, two, or four wild populations. To account for the effects of collection, we estimated the population size at each time step in the model and then reduced the density by an amount equal to either the number of adult females removed or a randomly generated number of hatchling snakes relative to potential clutch sizes (i.e., modifications happened across the entire adult or hatchling portion of the size distribution). In both cases, we restricted manipulations of the density function to only the adult or hatchling portion of the curve, depending on the collection method. For all collection scenarios, we set a starting population size of 60 individuals, a carrying capacity of 75 individuals, and used a survival function based on the median road density. We discarded the first 10 years as burn in to allow the uniform initial size distribution to stabilize before implementing the effects of collection. All analyses were conducted in R (R Core Team 2021).

Results

At median survival rates, various parameterizations of the fecundity kernel had marginal effects on λ in indigo snake populations (Figure 3). For example, if the probability of adult females breeding was 1.0, the difference in median λ between a 70% hatching rate (range = 0.94–1.29) and a 40% hatching rate (range = 0.86–1.15) was 0.098. Across various rates of breeding probability, a 10% increase in egg hatching rates led to, on average, a 0.03 increase in λ. Similarly, across different hatching rates, a 15% decline in breeding probability also led to a 0.03 decrease in λ, on average. However, it is worth noting that even though the magnitude of changes in λ were relatively small the values were generally near one, and lower breeding probability and hatching rate combinations led to a considerable proportion of IPM kernels with a λ value less than one (Figure 3).

Sensitivity and elasticity analyses for the fully stochastic kernel at median road densities and the stable size distribution for the mean kernel both indicated that there were multiple juvenile size groups as individuals approached reproductive maturity (Appendix E: Figure S1 and S2). Kernel level sensitivity suggested that changes to the kernel that impact the transitions of the most abundant size classes (i.e., 1–3-year-olds) into the adult size classes have the biggest relative effect on λ (Appendix E: Figure S1A). Furthermore, kernel level elasticity analyses suggested that changes to the survival-growth functions had larger effects on λ than changes to the fecundity functions (Appendix E: Figure S1B). The elasticity function for the survival-growth kernel again highlighted the importance of the juvenile age classes (Appendix E: Figure S1C). Finally, although not as important in the overall model, elasticity analyses on the reproductive kernel suggested that transitions into the reproductive size classes are most important (Appendix E: Figure S1D).

At high road densities, the median λ was 0.99 (range: 0.75–1.22), while median λ was positive at both median (1.06; range = 0.85–1.28) and low (1.09; range = 0.85–1.3) road densities (Figure 4). Across most combinations of road density and initial population size, extinction probabilities were near zero over a 100-year period. The only exception was the scenario with a high road density and low starting population size (15 individuals), which had a mean extinction probability of 0.21 (0.15–0.27) after 100 years. However, mean population sizes across all high road density scenarios slowly declined, while they were stable at median and low road densities (Figure 5). By the end of the modeling period, populations sizes, on average, were approximately 71% of the starting population size in all high road density scenarios, but there was also considerable variation across model runs (Figure 5). Finally, high collection rates of either adults or eggs quickly led to high extinction risk, while dividing the collection pressure across at least four populations had an extinction probability near zero (Figure 6). Furthermore, collection of adult female snakes led to higher extinction risk than egg collection as the collection rate was reduced (Figure 6).

Discussion

We combined a majority of the existing data describing important demographic processes in indigo snake populations to build an IPM that can be used to model the population dynamics for this imperiled snake. The modeling framework presents a flexible methodology that can be used to assess a variety of potential conservation and management scenarios for populations in both Georgia and Florida, especially when combined with existing spatially explicit assessments of habitat connectivity (Bauder et al. 2022). This research moves towards accomplishing one of the key goals of the Indigo Snake Recovery Plan by creating a model that can be used to better understand long-term population viability in wild indigo snake populations (USFWS 2019). This work also adds to the growing body of literature describing the demography of snake populations (e.g., Lind et al. 2005; Johnson et al. 2016; Tucker et al. 2020), which are often difficult to capture at rates sufficient for building this type of complex demographic model (Steen 2010).

Our results indicated that indigo snake populations experiencing minimal effects of habitat fragmentation from roads can persist for long periods of time with little risk of extirpation, even at low population sizes. However, at high road densities populations steadily (but slowly) declined, and population growth rates were less than one, on average. A plethora of research has shown that roads can have wide ranging impacts on the ecology, behavior, and population dynamics of indigo snakes (Hyslop et al. 2012; Bauder et al. 2021), other snake species (Enge and Wood 2002; Shine et al. 2004), and a broader variety of herpetofauna (Steen and Gibbs 2003; Beebee 2013; Howell and Seigel 2019). Roads are a near omnipresent landscape feature in the southeastern United States, even on protected lands, and urbanization and the associated road network are projected to increase across the southeastern U.S. throughout the 21st century (Terando et al. 2014). Many currently extant indigo snake populations will likely face increased pressure from roads (and urbanization more broadly) in the coming decades. Future research could expand the current modeling effort by identifying indigo snake populations that are likely to experience the most pressure from increasing road density (e.g., Fullman et al. 2020; Folt et al. 2022). We also note that the road densities considered here were based on areas that are likely to currently support indigo snake populations, and it is likely that populations impacted by extremely high road densities have already been extirpated. For example, Bauder et al. (2022) removed several potential conservation units because of their position in highly urban areas and lack of support from recent observations.

The road density and population size scenarios examined here were chosen to be representative of the factors affecting many indigo snake populations across their range. There are several important assumptions that should be considered when applying this model to specific population units identified by Bauder et al. (2022) or USFWS (2019). While our survival function directly accounted for anthropogenic effects through surrounding road density, we did not explicitly model other potential stressors that may impact survival, including habitat quality, disease prevalence (Chandler et al. 2019), or direct human persecution. For example, habitat quality is known to impact the survival of many species (Aubry et al. 2012; Josserand et al. 2017), and there is significant variation in habitat quality (and habitat use across a latitudinal gradient by indigo snakes; Chandler et al. 2022) across the southeastern U.S., primarily because of long-term fire suppression and winter prescribed fires (Brockway and Lewis 1997). Some of these effects are likely captured, at least in part, in the survival function but could be modeled explicitly in subsequent iterations of the modeling process.

Our results also assume that road characteristics are homogenous across space. However, this is unlikely to be the case in most indigo snake populations, and the actual effects of roads on populations could be spatially biased depending on the configuration of the road network (Jaeger et al. 2006; Eigenbrod et al. 2008). Furthermore, Hyslop et al. (2009) suggested that paved roads have a higher impact on indigo snake survival when compared to small, unpaved roads, which is supported by recent observation of indigo snake mortality events (Chandler, unpublished data). At high road densities, populations may be slowly limited to areas of unfragmented habitat, decreasing the overall population size relative to the total amount of habitat available (Eigenbrod et al. 2008; Böhm et al. 2016). These populations could then be more susceptible to environmental or demographic stochasticity that negatively impacts demographic rates (Caughley 1994). Adding a more detailed spatial analysis of landscape configuration to the modeling framework is an important next step.

We simulated the effects of different collection rates and strategies on indigo snake populations experiencing median effects of roads on survival. The model results strongly indicated that the highest collection rates (e.g., to completely support the captive breeding colony) would rapidly lead to extinction of wild populations. Splitting the collection rate across four populations lowered the extinction risk for individual populations, although even this scenario produced a non-zero extinction risk for the adult collection scenario. Furthermore, simulations suggested that collecting eggs was less likely to lead to extinction than collecting adults. We note that this assumes that nests can be reliably located in the wild or that holding gravid females in captivity until they deposit eggs has no effect on survival. We stress that initiation of any collection from wild populations should only be conducted with careful consideration of all potential outcomes (Edwards et al. 2019), especially considering the potentially complex effects of collection on herpetofauna (Wallace et al. 2013; Rose and Todd 2020). Integrating models describing the dynamics of wild, captive, and reintroduced (Folt et al. 2019) populations would provide critical insight into potential collection strategies.

Even though indigo snakes are relatively well-studied compared to many other snake species, there were still several key limitations in the available data describing indigo snake demography. First, there are no robust estimates of nest predation rates, although predation of nests has been noted on multiple occasions (Smith 1987; Stevenson et al. 2021). It is possible that in some years or at some sites nest predation rates could be substantially higher than those examined here, especially when considering observed predation rates on Gopher Tortoise (*Gopherus polyphemus*) nests in similar habitats (Landers et al. 1980; Smith et al. 2013; Dziadzio et al. 2016). Second, we ran simulations using a range of different initial population sizes because there are currently no published estimates of indigo snake abundance or density. The data likely exist to make such estimates in some populations that have been monitored for many years (e.g., on Fort Stewart; Stevenson et al. 2009). Third, we used a constant size distribution to initiate all modeling scenarios because there are no estimates of population-wide size distributions for indigo snakes, and juvenile indigo snakes are challenging to locate in the wild. Overall, these limitations highlight critical data gaps that could be addressed through future research.

Extant indigo snake populations continue to face a variety of threats despite widespread conservation and management of upland habitats in both Georgia and Florida (USFWS 2019). In populations that coincide with areas of high road densities, the long-term negative effects of road mortality on survival will likely cause population declines. Furthermore, indigo snake populations that experience additional mortality from roads are likely more susceptible to other future threats that impact survival. In such cases, identifying road crossing hotspots (e.g., Boyle et al. 2017) and establishing either barriers or wildlife crossing structures could be potential mitigation options. Future work re-examining site-specific risks and other potential threats based on the work here and in Chandler et al. (2022) and Bauder et al. (2022) would be an improvement on existing vulnerability metrics in the indigo snake SSA (USFWS 2019). Reintroductions have become an important part of ongoing conservation efforts for indigo snakes (Stiles et al. 2013). However, supporting a large and genetically diverse captive colony has proven challenging, and additional collection from wild populations will likely be needed to sustain the colony over the long term. For wild collection to be sustainable (i.e., have little chance of impacting wild populations), eggs should be collected from at least five wild populations that face minimal threats from roads and contain enough habitat to support robust population sizes.

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Table 1. Life history parameters that were modeled as part of a stochastic Integral Projection Model describing the population dynamics of Eastern Indigo Snakes (*Drymarchon couperi*). Sources provided were used either in full or in part as justification for parameters values, and most parameters were directly estimated from available indigo snake data. See equations provided in Appendix E: Table S1.

Parameter Description	Values	Source(s)
Asymptotic size (mm) in von Bertalanffy growth model (L_∞)	1.53–1.60	Chandler et al. (*In review*)
Growth coefficient in von Bertalanffy growth model (k)	0.99–1.45	Chandler et al. (*In review*)
Deviation in growth for individuals	0.03	Chandler et al. (*In review*)
Mortality rate scale coefficient (μ)	0.54–0.89	Bauder, unpublished data
Mortality rate coefficient for size (β_1)	-0.08–0.32	Bauder, unpublished data
Mortality rate coefficient for road density (β_2)	-0.19–0.002	Bauder, unpublished data
Slope of the size-dependent fecundity function (m)	0.04–0.9	Chandler, unpublished data; Wines et al. (2015)
Intercept of the size-dependent fecundity function (c)	-3.6–3.3	Chandler, unpublished data; Wines et al. (2015)
Size at reproductive maturity	1.23	Chandler, unpublished data
Probability of eggs hatching; drawn from a uniform distribution	0.4–0.7	Speake et al. (1987); Smith (1987); Wines et al. (2015)
Probability of female snakes breeding; drawn from a uniform distribution	0.7–1.0	Folt et al. (2019); Stevenson et al. (2021)
Mean hatchling size; drawn from a uniform distribution	0.364–0.384	Chandler, unpublished data
Deviation in hatchling size	0.035	Chandler, unpublished data

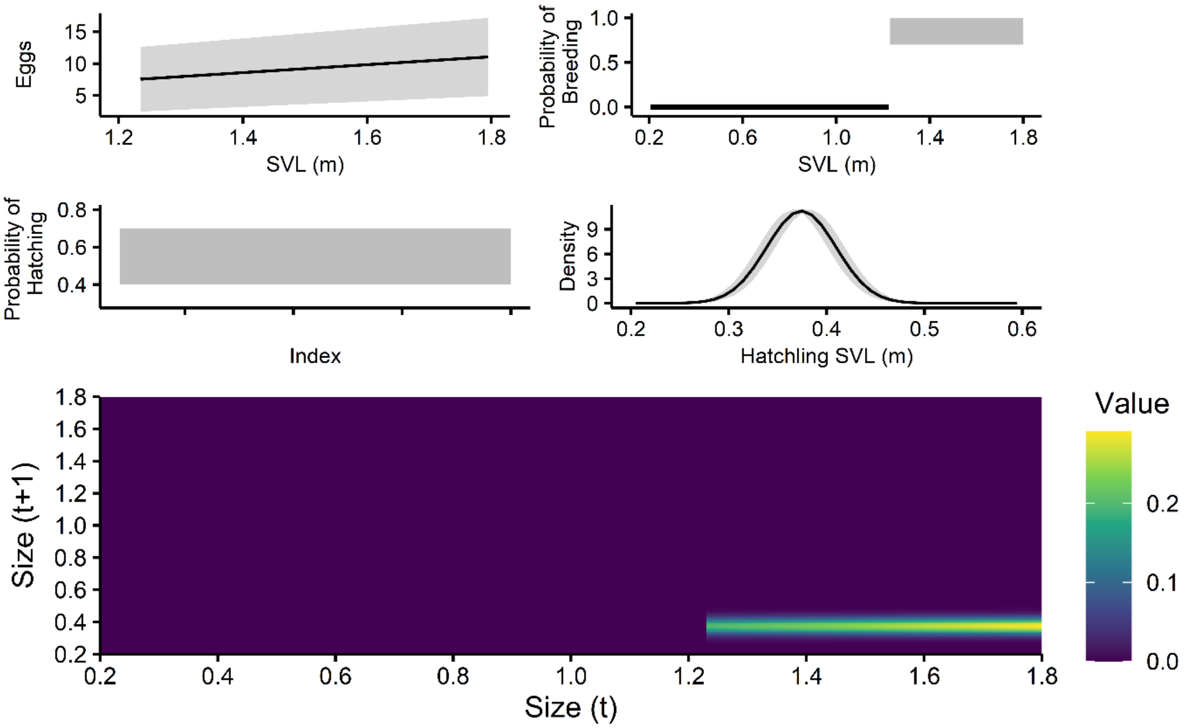

Figure 1. Demographic functions used to build the fecundity kernel of a stochastic Integral Projection Model for Eastern Indigo Snakes (*Drymarchon couperi*). Data sources and parameters values are provided in text and in Table 1.

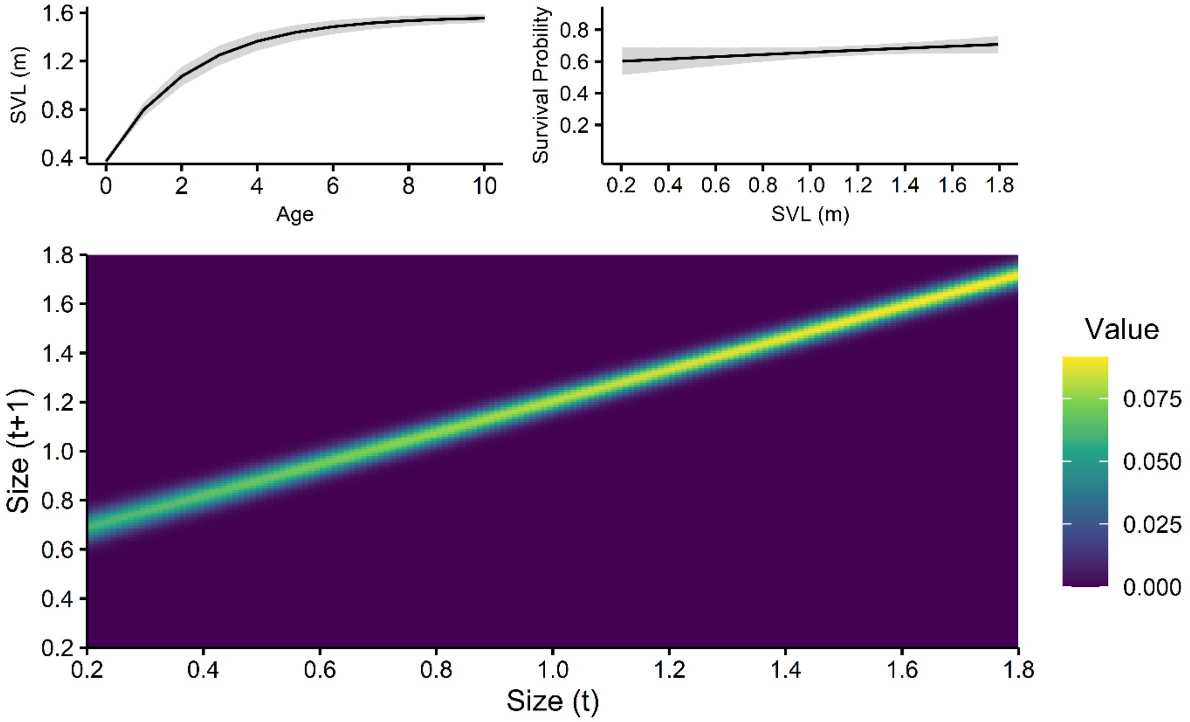

Figure 2. Demographic functions used to build the combined growth and survival kernel of a stochastic Integral Projection Model for Eastern Indigo Snakes (*Drymarchon couperi*). Data sources and parameters values are provided in text and in Table 1.

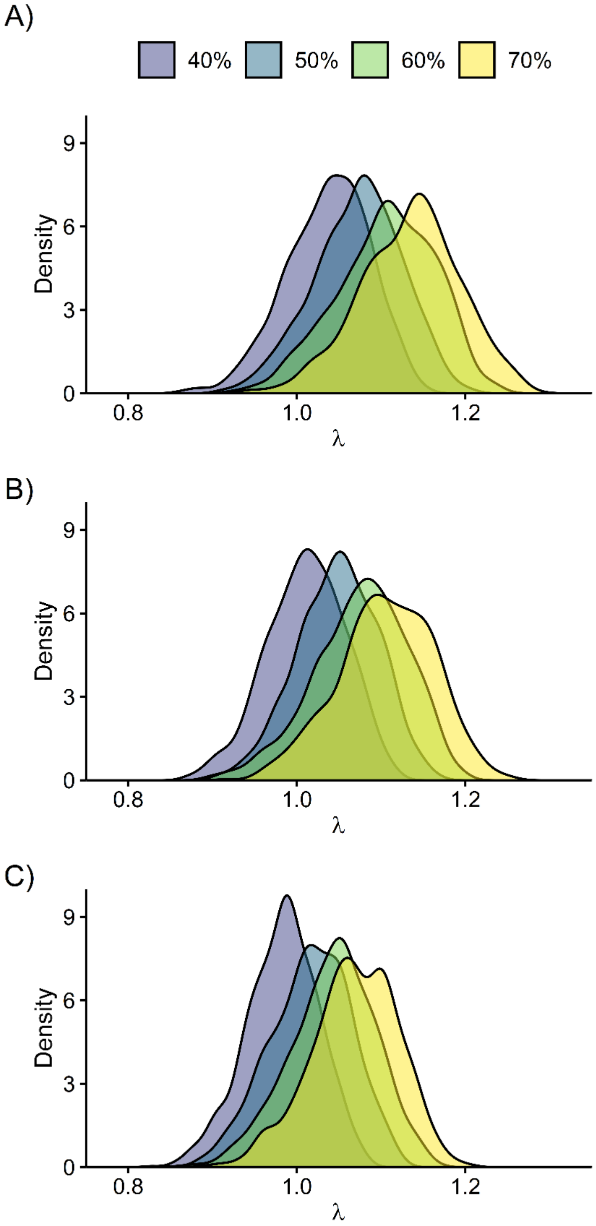

Figure 3. Population growth rates (λ) for various parameterizations of the fecundity kernel for an Integral Projection Model describing the population dynamics of Eastern Indigo Snakes (*Drymarchon couperi*). Fecundity kernels were parameterized with egg hatching rates ranging from 40–70% and with the percentage of females ranging from 100% (A) to 85% (B) to 70% (C). For all simulations, the survival function was held constant at the median value, while growth functions were allowed to vary stochastically.

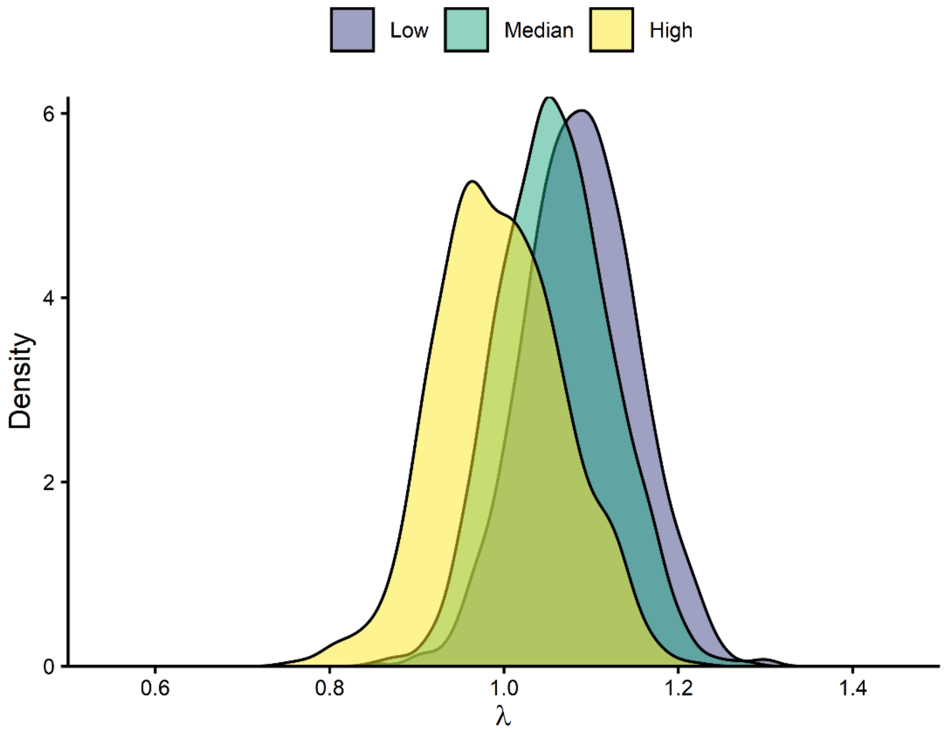

Figure 4. Population growth rates (λ) for different parameterizations of the growth and survival kernel for an Integral Projection Model describing the population dynamics of Eastern Indigo Snakes (*Drymarchon couperi*). Indigo snake survival was estimated across three representative road densities (low, median, and high) that correspond to observed densities in wild populations. Fecundity and growth parameters were allowed to vary stochastically across simulations.

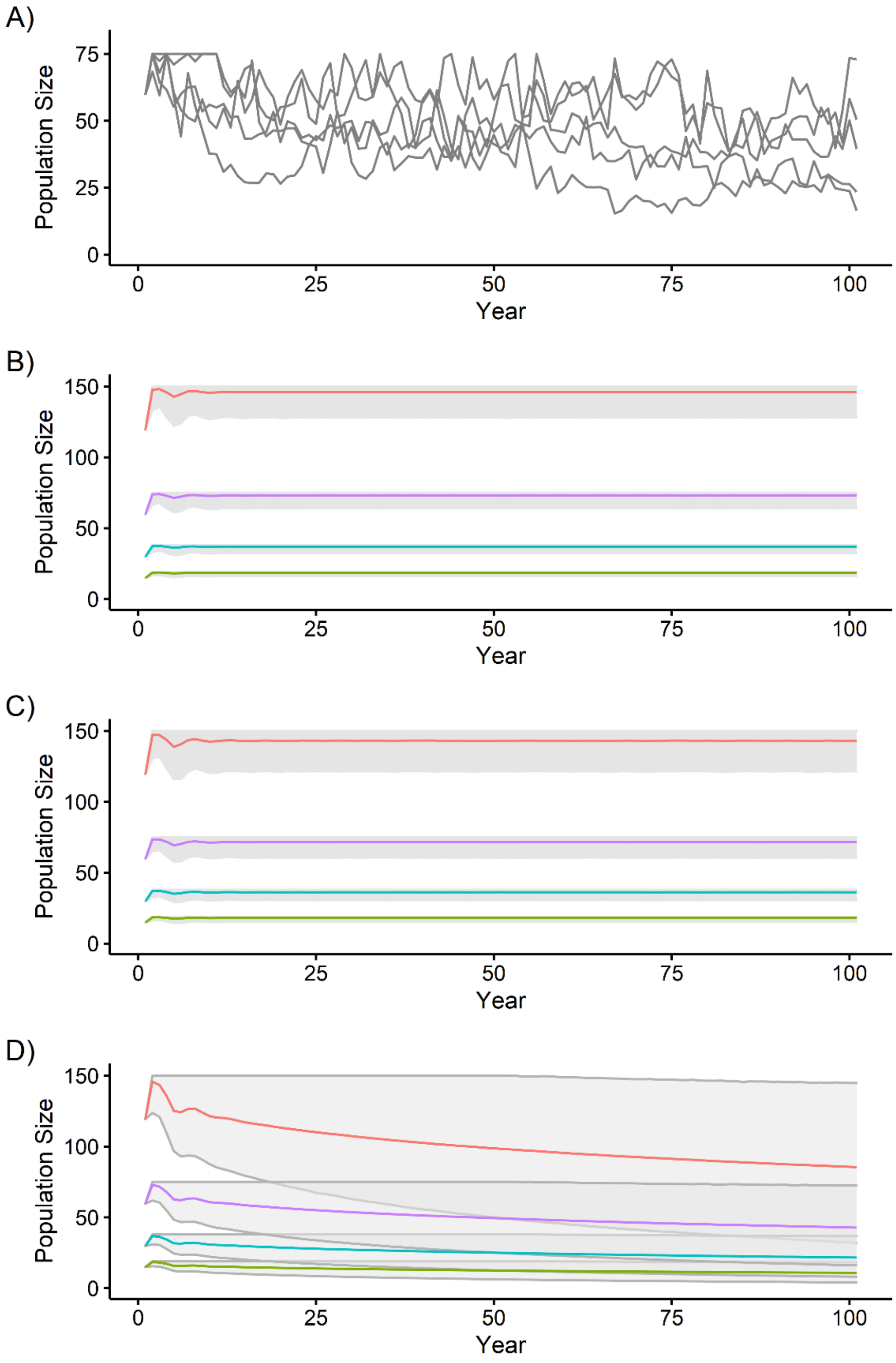

Figure 5. Population size estimates for representative Eastern Indigo Snake (*Drymarchon couperi*) populations with different initial population sizes and surrounding road densities.

Results were generated using an Integral Projection Model. Panel A shows variability across individual model runs for a single scenario (initial population size = 60 and a medium road density), while panels B, C, and D show the summarized results for low, medium, and high road density scenarios, respectively. Each line in B–D represents a different initial population size, and gray bands are 90th percentiles across all model runs.

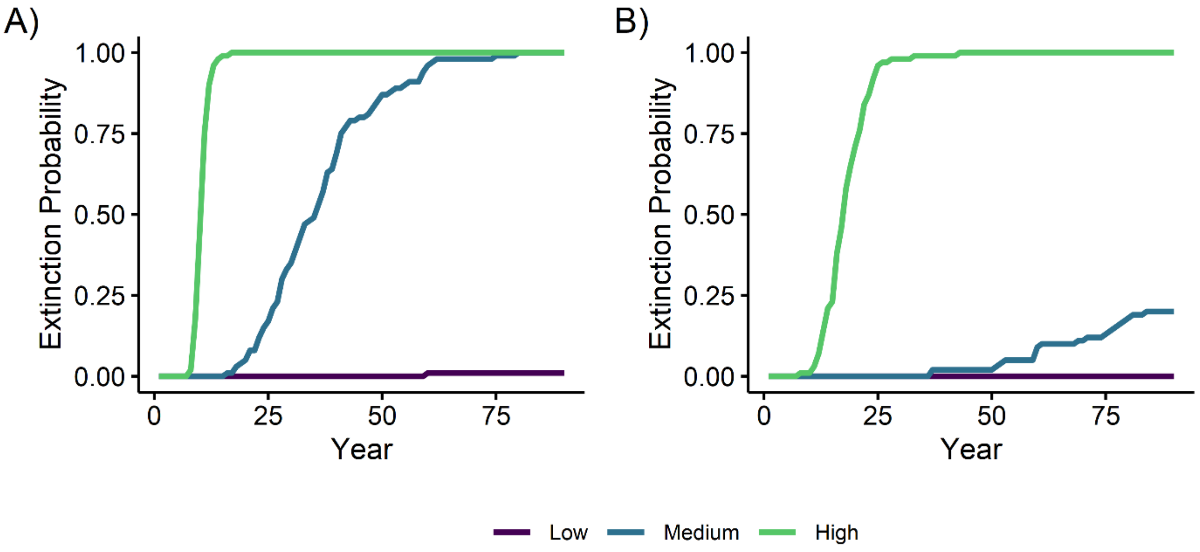

Figure 6. Extinction risk in Eastern Indigo Snake (*Drymarchon couperi*) populations under different levels of collection to support a captive breeding colony. Collection rates are based on values needed to support the captive breeding colony and under two different scenarios: adult female collection (A) and egg collection (B). High collection rates represent all collection from one population, medium collection rates represent collection from two populations, and low collection rates represent collection from four populations. All scenarios represent populations with a median road density and an initial population size of 60 individuals.

CONCLUSIONS

The southeastern United States is a globally important biodiversity hotspot, supporting high species richness across a variety of taxonomic groups. This region was once dominated by the longleaf pine ecosystem, but a long history of habitat loss and poor management has led to a precipitous decline in high-quality natural areas across this region (Frost 1993; Darracq et al. 2016; Ojha et al. 2021). Furthermore, high rates of fragmentation by roads, urban areas, and agricultural activities have reduced connectivity across much of the southeast, creating islands of natural habitats in an otherwise inhospitable landscape (Belote et al. 2017). Despite extensive conservation and management efforts by federal and state agencies, NGOs, and private landowners, many imperiled species throughout the southeast continue to decline. Increasingly prevalent stressors from a variety of global changes (e.g., urbanization; Terando et al. 2014) will continue to threaten natural communities across this region, necessitating effective use of limited conservation resources to meet these challenges head on.

In this work, I have described three main projects, split into four chapters, that each focus on a different aspect of conservation for Reticulated Flatwoods Salamanders or Eastern Indigo Snakes. Chapter 1 focuses on broadening our understanding of wetland hydrology and environmental characteristics using LiDAR-based habitat assessments. While this work has specific applications to flatwoods salamander conservation (e.g., informing survey efforts, directing habitat management, or guiding future translocations), it is also broadly applicable to our basic understanding of the ecology of organisms breeding in ephemeral wetlands as well as surface water storage capacity of these landscapes during flooding events. We now have the ability to quantify wetland characteristics in greater detail using coupled assessments of water level monitoring, wetland bathymetry, and other habitat metrics. Incorporating a more holistic view of wetland hydrology into species conservation programs will allow researchers to better understand important mechanistic links between environmental conditions and lifetime fitness (Semlitsch et al. 1988), while attempting to manage these systems in a changing environment.

Chapters 2 and 3 focus on identifying some of the potential effects of climate change on flatwoods salamander phenology and population viability. My results suggest that future shifts in phenology are unlikely to make the current situation for flatwoods salamanders worse, at least in the short term (i.e., the next several decades). However, the current situation is generally poor, and the hydrology in many breeding wetlands already appears less suitable than during the preceding century (Chandler et al. 2016). The results from Chapter 2 highlight that there are likely to be frequent potential negative interactions between salamander phenology and wetland hydrology. These negative interactions had strong effects on long-term population viability when compared to just hydroperiod effects alone as shown in Chapter 3. The magnitude of the effects of interacting phenology and hydrology is challenging to identify, and future work should focus on quantifying how various interactions between hydrology and phenology impact overall reproductive success. Overall, small populations of flatwoods salamanders, similar to those examined in this work, are likely to face relatively high extinction risks from repeated reproductive failure and marginal breeding years over the next several decades. Maintaining connectivity across multiple breeding sites with varying hydrological characteristics will be an essential tool to reduce local extinction risk.

In Chapter 4, I created a flexible population modeling framework for indigo snakes using demographic data from both wild and captive populations. My results highlighted how landscape characteristics that impact demographic processes (e.g., road density effects on survival) can have important implications for long-term population stability. I also used the model to demonstrate that at least five indigo snake populations, facing minimal road effects, were needed to sustain collection for the female component of the captive breeding colony. These examples point to the importance of using a population modeling framework to support conservation efforts for this charismatic species. This work is ongoing, and the next steps will be to combine the modeling framework presented here with the work of Chandler et al. (2022) and Bauder et al. (2022) to examine site-specific scenarios across the indigo snake's distribution.

There are a variety of important points that can be taken from the preceding work, both for the two focal species and for reptiles and amphibians more broadly. For flatwoods salamanders, conservation efforts should focus on 1) maintaining habitat quality in wetlands through prescribed fire, woody vegetation removal, and removal of duff accumulations, 2) restoring and maintaining clusters of wetlands that allow populations to undergo natural processes of colonization and extinction, and 3) identify ways to increase breeding success through marginal years, whether through upland vegetation (Jones et al. 2018) or hydrologic management. Furthermore, because of historic range contractions (O'Donnell et al. 2017), translocations will continue to be an important aspect of flatwoods salamander conservation efforts. Translocations should be supported using both the tools described here (e.g., vegetation and hydrologic assessments and population modeling) and other techniques (e.g., conservation genetics) to enhance the potential for meaningful contributions to species recovery. Flatwoods salamanders have declined to the point where future persistence is not assured, especially considering the threats facing freshwater ecosystems. If implemented successfully, the conservation efforts described above can minimize the probability of extinction at both local and landscape scales.

Indigo snakes have been the focus of active conservation efforts for several decades, but populations are generally considered to still be declining in many parts of their range. However, assessments of the species status, at both fine and broad geographic scales, have been hampered by a lack of quantitative spatial planning tools. To build on the work presented here, future research should focus on filling important data gaps, especially generating robust estimates of nest success rates and abundance metrics. Management efforts for indigo snakes should focus on 1) improving habitat quality through prescribed fire and tree or understory plantings, 2) maintaining and improving connectivity to reduce the negative impacts of fragmentation, especially within large, protected landscapes, and 3) maintaining or restoring Gopher Tortoise populations, particularly in the northern portion of the indigo snake range (Hyslop et al. 2009). Finally, ongoing reintroduction efforts are an important aspect of indigo snake conservation and future efforts should be made to link the population model described here with existing assessments of reintroduced populations (Folt et al. 2019) to create a decision framework that identifies suitable strategies for managing captive, reintroduced, and wild populations as a single, cohesive unit.

In the coming years, conservation and management programs in the southeastern U.S. focusing on rare herpetofauna will face unprecedented challenges as global change continues through a variety of pathways. These changes will likely fundamentally impact conservation programs in many ways, and stakeholders should be prepared to shift strategies to combat previously unexpected outcomes or synergies between threats. Planning for the potential effects of future changes can be difficult but examining a range of potential scenarios can offer insights into how current situations are most likely to change. Furthermore, long-term monitoring programs are needed to identify both key demographic rates and the effects of both stressors and corresponding management responses. In the southeast, there is an abundance of available knowledge detailing best practices for habitat management that can maintain or restore upland and aquatic systems. This work should be a top priority to promote robust populations that are buffered against some of the more uncertain global changes.

A history of habitat loss has led to range contractions across many species in the southeast (these effects often continue today), and a severely fragmented landscape generally prevents herpetofauna from reclaiming portions of their historic range, even if suitable habitat exists. To combat these processes, reintroductions or translocations have become key aspects in many conservation programs. However, moving animals across the landscape should only be attempted with strong scientific support that identifies how projects can be completed with the highest probabilities of success while considering a variety of factors (e.g., effects on source populations, potential for captive breeding, and population genetics). Furthermore, the initial threats that led to local extirpation must be addressed in perpetuity (i.e., a need for long-term management plans). These efforts, if ultimately successful, can increase the overall resiliency for imperiled species and boost the total number of extant populations, potentially impacting recovery goals.

Finally, this work highlights significant and meaningful deficiencies in our basic natural history data. Importantly, flatwoods salamanders and indigo snakes are two of the most well-studied reptile and amphibian species in the southeast, but a lack of basic knowledge about key demographic rates or relationships between environmental characteristics and population biology persists. For many other species, we know next to nothing about their natural history and how it relates to environmental conditions. This lack of knowledge can make it difficult if not impossible to enact meaningful conservation efforts. Using basic life history theory and an understanding of historic disturbance regimes can be powerful tools to assess how populations will respond to different stressors (e.g., Brooks and Kindsvater 2022). Models provide useful guidance and the ability to compare potential scenarios for conservation programs, but they fundamentally rely on accurate inputs, often of basic natural history information. Natural history research is perpetually underfunded and underappreciated in the published literature, but it is of high value when considering the realities of implementing on-the-ground conservation projects.

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APPENDIX A

All material associated with Chapter 1. Additional details about study wetlands and Reticulated Flatwoods Salamanders (*Ambystoma bishopi*). Additional details of landscape topographic metrics and additional wetland metrics that were used to predict median flooded areas in pine flatwoods wetlands without any monitoring well data. Additional details of analyses used to generate stage–area relationships for pine flatwoods wetlands in the Florida panhandle.

All wetlands included in this study are located in the East Bay Flatwoods on Eglin Air Force Base, one of the best remaining examples of the pine flatwoods ecosystem. The East Bay Flatwoods is an actively managed landscape, and Eglin Air Force Base has an active prescribed fire program. Poorly drained, sandy soils that support the presence of numerous wetlands across the study area are primarily composed of Chipley, Kureb, Leon, and Rutlege soils (Soil Survey Staff 2016). Vegetation communities within wetlands are generally made up of a Longleaf (*Pinus palustris*) and Slash Pine (*Pinus elliottii*) overstory, with a diverse understory of grasses and forbs. The understory is commonly dominated by Pineland Threeawn (also known as wiregrass, *Aristida stricta*; Chandler 2015), but the highly diverse herbaceous community includes several plants that are rare. Wetlands in this ecosystem are most likely to be inundated from the late fall through early spring when evapotranspiration rates are low and then typically dry during the summer months, despite an increase in precipitation (Chandler et al. 2016).

Figure S1. Images of pine flatwoods wetlands showing differences in vegetation structure (Photo Credits: Brandon Rincon [top] and Houston Chandler [bottom]).

Flatwoods salamanders are small ambystomatid salamanders that are endemic to mesic pine flatwoods of the southeastern U.S. Coastal Plain. However, flatwoods salamanders have experienced severe population declines and range contractions throughout their range and are now listed on the U.S. Endangered Species List (USFWS 2009). These salamanders depend on herbaceous vegetation during multiple portions of their life cycle. Furthermore, the total amount of herbaceous vegetation within a wetland has been shown to be positively correlated with both site occupancy and effective population size (Brooks et al. 2019; Wendt et al. 2021). Because of a relatively long larval period (11–18 weeks), flatwoods salamanders are susceptible to complete reproductive failure during both drought years and years with an intermittent hydroperiod (Chandler et al. 2016). Other hydrologic factors, including the timing of wetland filling and the recession rate as salamanders near metamorphosis, may also impact reproductive success (Chandler et al. 2017).

Figure S2. Adult flatwoods salamander at a breeding wetland (Photo Credit: Houston Chandler).

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Table S1. Landscape metrics calculated for the East Bay Flatwoods on Eglin Air Force Base, Florida using a high-resolution digital elevation model. Metrics were summarized as mean values for delineated pine flatwoods wetlands in the study area. An asterisk represents variables that were dropped from the final analysis due to collinearity.

Metric	Description
Deviation from Mean Elevation*	Difference in elevation between a pixel and the mean elevation of surrounding pixels normalized by standard deviation. Calculated with a 100m radius circular buffer around each pixel.
Slope*	Slope gradient for each pixel
Topographic Wetness Index	Metric incorporating upstream contributing area and slope to measure wetness
Ruggedness Index*	Elevation difference between a pixel and all adjacent pixels calculated as the root mean square deviation
Contributing Area	Flow accumulation calculated using the D8 algorithm
Downslope Distance*	Distance of each pixel to the nearest stream pixel via downslope flowpaths
Downslope Index	Measure of the slope gradient between a pixel and some downslope location on the flowpath based on a specified elevation drop
Plan Curvature	Second derivative of the topographic surface; rate of change of aspect along a contour line
Profile Curvature*	Second derivative of the topographic surface; rate of change in the slope along a flowline
Height above Nearest Drainage	Elevation of each pixel above the nearest stream pixel
Area	Maximum flooded area of each wetland
Elevation	Mean elevation for each wetland
Elevation Difference	Difference between mean wetland elevation and the mean elevation within a 50-m buffer surrounding the wetland

Table S2. Correlation matrix for all variables included in the landscape analysis. An asterisk indicates variables that were dropped from the final model due to collinearity. Abbreviations for all variables are: Area = maximum wetland area, Elevation = mean elevation, Slope = slope, TWI = Topographic Wetness Index, DS Index = Downslope Index, Ruggedness = Ruggedness Index, DS Dis = Downslope Distance, DEV = Deviation from Mean Elevation, Prof Curve = Profile Curvature, Plan Curve = Plan Curvature, HAND = Height above Nearest Drainage, Catch Area = Contributing Area, Elevation Dif = the difference between wetland elevation and the elevation in a 50 m buffer around the wetland.

	Area	Elevation	Slope*	TWI	DS Index	Ruggedness*	DS Dis*	DEV*	Prof Curve*	Plan Curve	HAND	Catch Area	Elevation Dif
Area	1.0	0.1	0.6	-0.6	0.2	0.6	-0.2	0.7	0.4	-0.3	-0.2	0.2	0.3
Elevation	0.1	1.0	-0.3	0.2	-0.3	-0.3	0.1	-0.2	-0.2	0.0	-0.1	-0.5	0.2
Slope*	0.6	-0.3	1.0	-1.0	0.3	1.0	-0.4	0.8	0.8	0.0	-0.2	0.1	0.4
TWI	-0.6	0.2	-1.0	1.0	-0.4	-1.0	0.4	-0.8	-0.9	0.0	0.3	-0.1	-0.3
DS Index	0.2	-0.3	0.3	-0.4	1.0	0.4	-0.3	0.4	0.4	0.0	-0.5	0.5	0.1
Ruggedness*	0.6	-0.3	1.0	-1.0	0.4	1.0	-0.4	0.8	0.9	0.0	-0.2	0.1	0.4
DS Dis*	-0.2	0.1	-0.4	0.4	-0.3	-0.4	1.0	-0.6	-0.2	0.3	0.7	-0.5	0.0
DEV*	0.7	-0.2	0.8	-0.8	0.4	0.8	-0.6	1.0	0.6	-0.3	-0.4	0.4	0.2
Prof Curve*	0.4	-0.2	0.8	-0.9	0.4	0.9	-0.2	0.6	1.0	0.3	-0.2	0.0	0.1
Plan Curve	-0.3	0.0	0.0	0.0	0.0	0.0	0.3	-0.3	0.3	1.0	0.2	-0.2	-0.2
HAND	-0.2	-0.1	-0.2	0.3	-0.5	-0.2	0.7	-0.4	-0.2	0.2	1.0	-0.3	0.0
Catch Area	0.2	-0.5	0.1	-0.1	0.5	0.1	-0.5	0.4	0.0	-0.2	-0.3	1.0	-0.2
Elevation Dif	0.3	0.2	0.4	-0.3	0.1	0.4	0.0	0.2	0.1	-0.2	0.0	-0.2	1.0

Table S3. Model results for Equation 1 in 12 pine flatwoods wetlands that were known to be partially flooded when LiDAR data were collected. We used this equation to estimate portions of the stage–area curve that were predicted to be flooded during data collection.

ID	Estimate for p Parameter	Standard Error	t value	P value
1	3.51	0.10	36.6	< 0.001
2	3.30	0.06	53.8	< 0.001
14	2.39	0.05	52.2	< 0.001
15	4.43	0.07	68.0	< 0.001
16	2.02	0.04	51.5	< 0.001
18	5.54	0.05	107.6	< 0.001
30	4.34	0.05	91.4	< 0.001
31	3.65	0.08	48.0	< 0.001
33	2.25	0.08	29.7	< 0.001
36	1.55	0.02	69.9	< 0.001
112	8.90	0.21	43.2	< 0.001
202	2.54	0.02	130.7	< 0.001

Table S4. The number of flooded area values for each wetland that were estimated using Equation 1 (i.e., were less than the predicted flooded area when the LiDAR data were collected), and the numbers of flooded area values that were measured using wetland bathymetry. These represent all daily flooded area values across four flatwoods salamander breeding seasons (November–May, 2015–2019). We also present the mean and standard deviation of the estimated flooded areas, represented as percentages of the maximum flooded area recorded during this period.

ID	# of Area Values Estimated	# of Area Values Measured	Percent Estimated	Percent of Maximum Flooded Area
1	725	88	89.2	12.8 ± 11.0
2	305	714	29.9	3.7 ± 4.0
12	0	798	-	-
14	183	696	20.8	12.4 ± 10.1
15	571	481	54.8	2.5 ± 2.7
16	145	216	40.2	9.6 ± 8.0
18	340	144	70.2	4.1 ± 3.0
21	0	639	-	-
30	378	696	35.2	1.7 ± 1.6
31	663	431	60.6	10.2 ± 7.9
33	218	433	33.5	9.4 ± 7.8
36	210	707	22.9	10.4 ± 6.1
112	828	360	69.7	2.8 ± 3.4
202	406	624	39.4	9.9 ± 7.3

Table S5. Model selection results for linear models relating topographic metrics to median flooded areas in 14 pine flatwoods wetlands. Single-factor and two-factor models were assessed separately.

Landscape Metric	BIC	Adjusted R^2
Single-factor Models		
Area	5.9	0.25
Elevation	7.7	0.14
Plan Curve	8.1	0.12
Catch Area	8.2	0.11
TWI	8.5	0.09
DS Index	10.3	-0.03
Elevation Difference	10.8	-0.07
HAND	11.0	-0.08
Two-factor Models		
Area + Elevation	1.9	0.49
Area + Catch Area	6.1	0.31
Elevation + Plan Curve	6.8	0.28
Area + Plan Curve	6.9	0.27
Plan Curve + TWI	7.6	0.23
Catch Area + TWI	8.2	0.20
Area + DS Index	8.3	0.20
Area + TWI	8.4	0.19
Area + HAND	8.4	0.19
Plan Curve + Catch Area	8.4	0.19
Area + Elevation Difference	8.5	0.18
Elevation + TWI	8.6	0.17
Elevation + Catch Area	9.5	0.12
Elevation + Elevation Difference	9.5	0.12
Plan Curve + DS Index	9.8	0.10
Catch Area + Elevation Difference	10.0	0.09
Elevation + DS Index	10.3	0.07
Elevation + HAND	10.3	0.07
Plan Curve + HAND	10.6	0.05
Catch Area + HAND	10.6	0.05
Plan Curve + Elevation Difference	10.7	0.04
Catch Area + DS Index	10.8	0.03
TWI + HAND	10.9	0.02
TWI + DS Index	11.1	0.01
TWI + Elevation Difference	11.2	0.01
DS Index + Elevation Difference	12.7	-0.11
DS Index + HAND	12.7	-0.11
Elevation Difference + HAND	13.4	-0.16

APPENDIX B

Additional details about Reticulated Flatwoods Salamander (*Ambystoma bishopi*) sampling effort for data used in Chapters 2 and 3.

Table S1. Dates of operation for two drift fences on Eglin Air Force Base in Okaloosa County, Florida. Ponds were completely encircled, but on a few nights in 2010–2011, we ran them as partial fences. Fences were operated continuously during dates shown below during the 2011–2012, 2012–2013, 2014–2015, 2016–2017, and 2017–2018 seasons. The 2010–2011 season was not a continuous run. The 2013–2014 season was run continuously until 04/30/2014, but then run on 19 nights until full closure on 05/31/2014. The 2015–2016 season was run continuously until 12/22/2015, then reduced to five days a week between 12/27/2015 – 03/18/2016, and finally run on 15 nights until full closure on 05/04/2016. Only partial fences were run on 3/31/2020.

Season	Pond 4	Pond 5
2010–2011	11/02–02/27	12/12–02/27
2011–2012	10/31–03/23	10/31–03/23
2012–2013	10/29–03/12	10/29–03/12
2013–2014	10/06–05/31	10/06–05/31
2014–2015	09/13–03/29	09/13–03/29
2015–2016	10/12–05/04	10/12–05/04
2016–2017	11/08–12/20 & 3/24–05/24	11/08–12/20 & 3/24–05/24
2017–2018	10/22–12/19 & 04/22	10/22–12/19 & 04/22
2018–2019	09/15–12/09	09/15–12/09
2019–2020	10/18–12/18 & 03/31	10/18–12/18 & 03/31

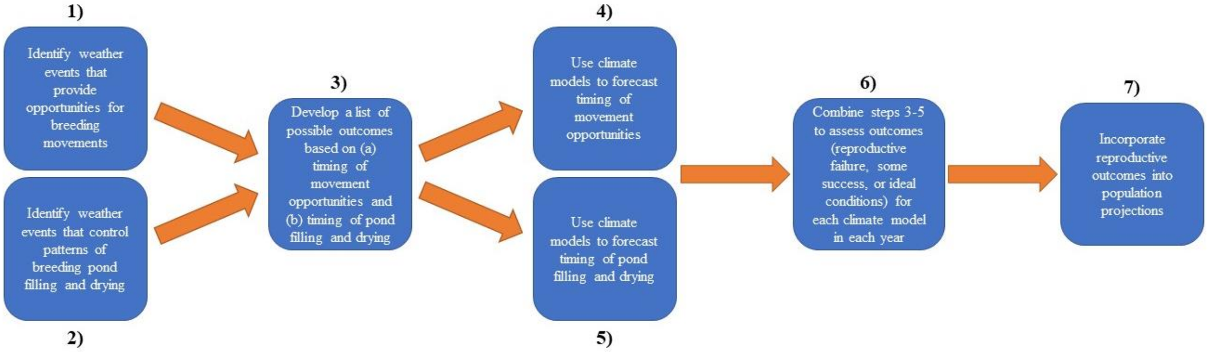

Figure S1. Conceptual diagram describing workflow for Chapters 2 and 3, focusing on climate change impacts on Reticulated Flatwoods Salamander (*Ambystoma bishopi*) phenology and population viability. Chapter 2 deals with salamander phenology (steps 1, 3, and 4). These results are combined with the hydrologic model presented in Chandler et al. (*In prep*) (steps 2 and 5) to estimate outcomes under future climate scenarios (step 6). Finally, an Integral Projection Model is used to understand how reproductive outcomes projected under different climate scenarios impact population viability (step 7).

APPENDIX C

All material associated with Chapter 2. Additional details about salamander phenology and future breeding season characteristics.

Table S1. Characteristics of potential movement events for Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) on Eglin Air Force Base, Florida based on three Global Circulation Models and two representative concentration pathways. Values represent means ± standard deviations.

Decade	Move Number	Mean Min Temp (°C)	Mean Total PPT (mm)	Move Number	Mean Min Temp (°C)	Mean Total PPT (mm)
	HadGEM2-CC RCP 4.5			HadGEM2-CC RCP 8.5		
2030s	6.3 ± 1.0	11.9 ± 1.4	273.6 ± 183.3	5.7 ± 1.4	12.8 ± 1.7	220.8 ± 123.8
2040s	5.4 ± 1.4	13.1 ± 1.8	212.5 ± 103.9	6.4 ± 1.9	13.0 ± 1.8	229.9 ± 68.8
2050s	6.5 ± 2.2	12.5 ± 1.1	253.8 ± 80.2	6.6 ± 1.8	13.0 ± 1.7	353.3 ± 67.4
2060s	6.0 ± 1.1	13.2 ± 2.3	218.7 ± 64.2	6.8 ± 0.9	14.2 ± 1.6	242.9 ± 118.7
2070s	6.7 ± 1.7	13.1 ± 1.2	274.4 ± 80.7	5.7 ± 1.6	13.6 ± 1.5	240.5 ± 55.5
2080s	6.0 ± 1.2	12.5 ± 1.5	219.4 ± 104.8	5.1 ± 1.9	14.4 ± 2.3	307.0 ± 151.5
2090s	6.5 ± 1.0	14.2 ± 1.1	261.3 ± 99.0	4.3 ± 1.2	14.1 ± 1.6	337.8 ± 134.1
Total	6.2 ± 1.5	12.9 ± 1.6	244.8 ± 106.6	5.8 ± 1.7	13.6 ± 1.8	259.5 ± 105.8
	HadGEM2-ES RCP 4.5			HadGEM2-ES RCP 8.5		
2030s	5.5 ± 2.1	11.9 ± 1.9	256.5 ± 130.5	5.6 ± 1.9	13.2 ± 2.0	220.8 ± 123.8
2040s	5.4 ± 2.1	13.0 ± 1.5	337.5 ± 143.9	5.8 ± 1.3	13.0 ± 1.8	229.9 ± 68.8
2050s	6.3 ± 1.8	12.8 ± 1.5	290.9 ± 107.4	4.7 ± 0.8	13.7 ± 1.0	353.3 ± 67.4
2060s	6.2 ± 1.1	12.9 ± 1.3	313.1 ± 91.5	5.7 ± 1.4	12.8 ± 1.9	242.9 ± 118.7
2070s	5.8 ± 1.7	13.6 ± 1.9	372.0 ± 128.9	6.0 ± 1.2	14.3 ± 1.7	240.5 ± 55.5
2080s	5.9 ± 1.7	14.6 ± 1.5	326.6 ± 156.6	5.0 ± 1.4	13.6 ± 1.5	307.0 ± 151.5
2090s	5.8 ± 1.4	12.5 ± 1.1	284.9 ± 172.2	5.1 ± 1.6	12.8 ± 1.5	337.8 ± 134.1
Total	5.8 ± 1.7	13.0 ± 1.7	311.6 ± 134.2	5.4 ± 1.4	13.4 ± 1.7	276.0 ± 115.9
	CCSM4 RCP 4.5			CCSM4 RCP 8.5		
2030s	5.7 ± 1.3	11.2 ± 1.9	272.5 ± 125.1	5.5 ± 1.3	11.6 ± 1.3	273.8 ± 155.3
2040s	5.9 ± 1.4	11.7 ± 0.8	271.9 ± 128.6	5.4 ± 1.0	12.6 ± 1.1	287.8 ± 162.1
2050s	6.0 ± 1.4	12.4 ± 1.0	284.8 ± 156.6	4.8 ± 1.6	12.7 ± 2.1	353.5 ± 179.1
2060s	6.0 ± 1.5	11.8 ± 1.5	295.2 ± 114.5	5.8 ± 1.1	12.9 ± 1.6	277.5 ± 124.0
2070s	6.0 ± 1.7	12.6 ± 2.1	289.2 ± 158.2	6.4 ± 1.5	12.2 ± 1.2	247.0 ± 99.7
2080s	5.5 ± 1.6	12.3 ± 1.6	262.3 ± 114.3	6.4 ± 1.3	13.1 ± 1.6	295.5 ± 110.3
2090s	5.6 ± 1.6	12.8 ± 1.6	251.4 ± 153.2	5.4 ± 2.0	13.7 ± 0.9	362.2 ± 126.3
Total	5.8 ± 1.5	12.1 ± 1.6	275.3 ± 131.7	5.7 ± 1.5	12.7 ± 1.5	294.5 ± 137.2

Table S2. Predicted characteristics of Reticulated Flatwoods Salamander (*Ambystoma bishopi*) breeding seasons on Eglin Air Force Base from 2030–2099. Predictions are based on three Global Circulation Models each with two representative concentration pathways (emission scenarios) and a hydrologic model created using the same climate data.

Pond 4	CCSM4 RCP4.5	CCSM4 RCP8.5	HadGEM2-ES RCP4.5	HadGEM2-ES RCP8.5	HadGEM2-CC RCP4.5	HadGEM2-CC RCP8.5
Unsuitable	33	27	20	21	19	13
Winter Metamorphosis	15	14	16	20	8	15
Flooded at Immigration	5	12	8	14	5	7
Flooding/Drying	23	27	26	27	35	41
Short Hydroperiod	17	19	15	17	19	18
Ideal	5	3	12	6	9	8
Pond 5						
Unsuitable	38	31	22	22	22	15
Winter Metamorphosis	14	13	19	22	9	14
Flooded at Immigration	5	10	8	10	3	6
Flooding/Drying	17	24	26	26	31	40
Short Hydroperiod	13	16	15	22	21	23
Ideal	6	2	9	8	9	5

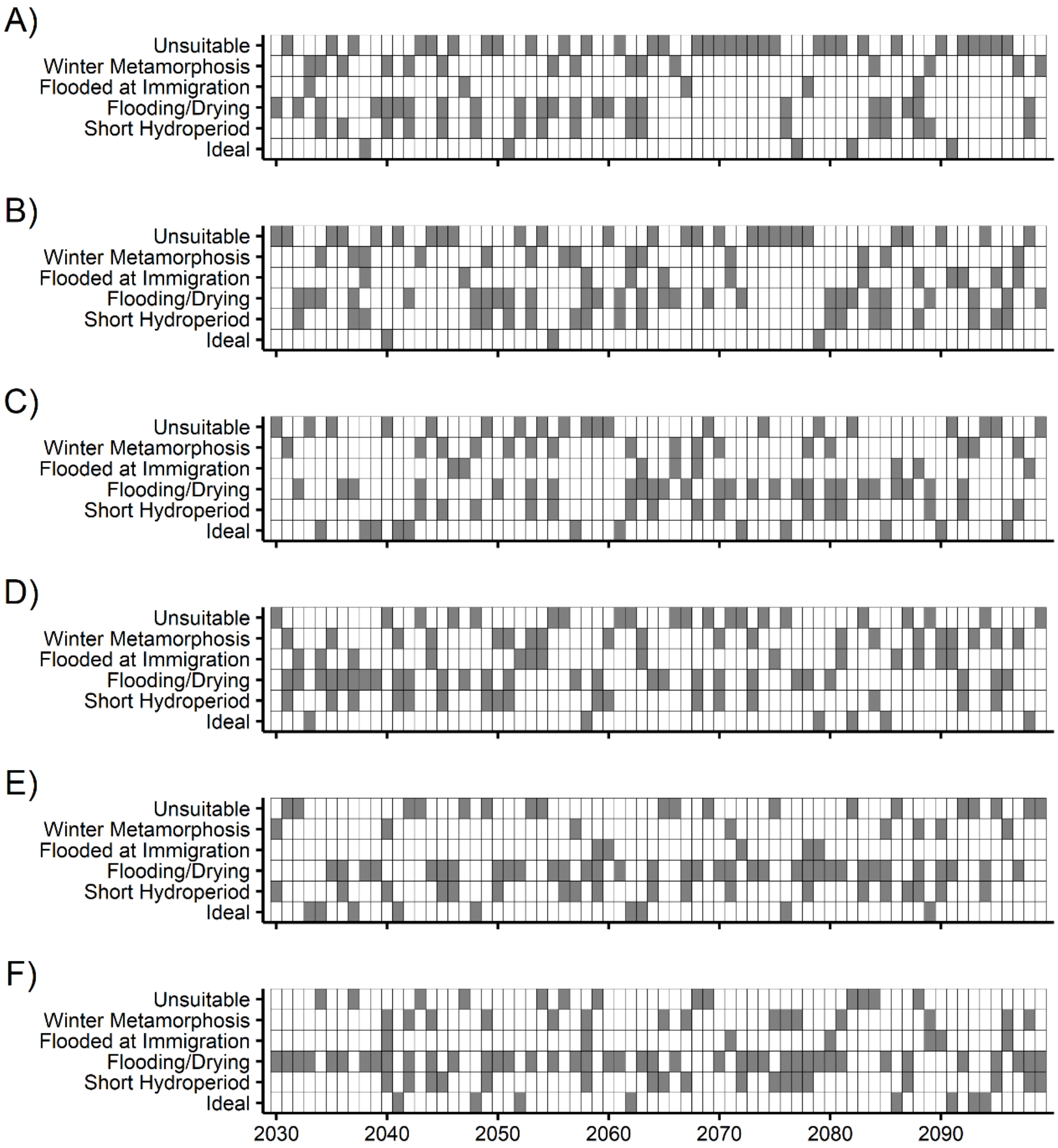

Figure S1. Predicted conditions during future Reticulated Flatwoods Salamander (*Ambystoma bishopi*) breeding seasons for a single breeding site (Pond 4) based on six global circulation model and representative concentration pathways (emission scenario) combinations (A: CCSM4 RCP 4.5; B: CCSM4 RCP 8.5; C: HadGEM2-ES RCP 4.5; D: HadGEM2-ES RCP 8.5; E: HadGEM2-CC RCP 4.5; F: HadGEM2-CC RCP 8.5).

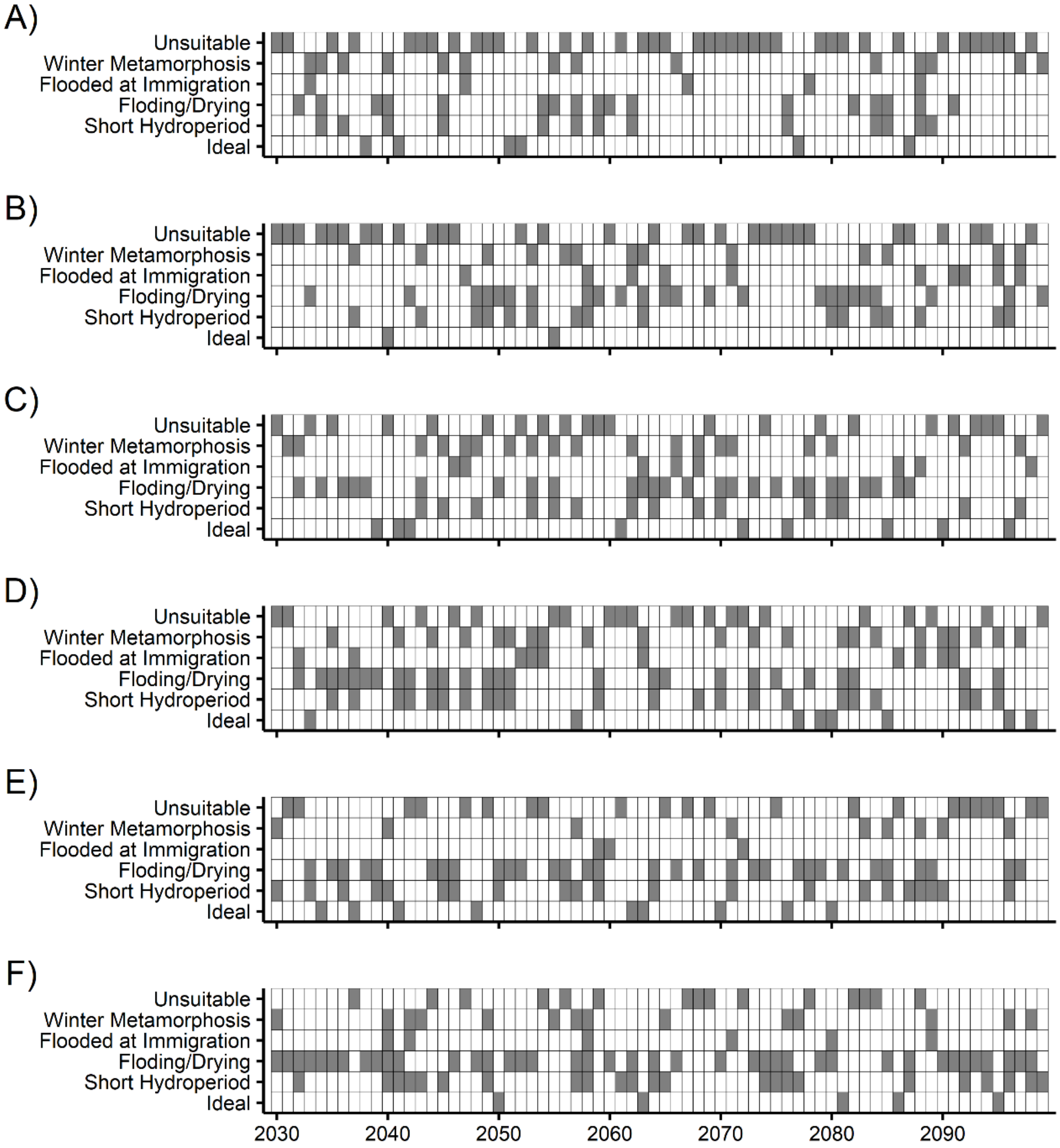

Figure S2. Predicted conditions during future Reticulated Flatwoods Salamander (*Ambystoma bishopi*) breeding seasons for a single breeding site (Pond 5) based on six global circulation model and representative concentration pathways (emission scenario) combinations (A: CCSM4 RCP 4.5; B: CCSM4 RCP 8.5; C: HadGEM2-ES RCP 4.5; D: HadGEM2-ES RCP 8.5; E: HadGEM2-CC RCP 4.5; F: HadGEM2-CC RCP 8.5).

APPENDIX D

All material associated with Chapter 3. Additional details about flatwoods salamander Integral Projection Model, including demographic equations, starting densities, stable size distributions, and elasticity and sensitivity plots.

Table S1. Equations describing demographic processes used to build an Integral Projection Model for Reticulated Flatwoods Salamanders (*Ambystoma bishopi*). Parameter values are listed in Chapter 3: Table 1.

Process	Equation
Mean Individual Growth	$SVL_{t+1} = SVL_t + (L_\infty - SVL_t) * (1 - e^{-k})$
Growth with Individual Variation	$N(SVL_{t+1}, 3)$ or $N(SVL_{t+1}, 1)$
Size Dependent Survival	$\frac{1}{1 + e^{-(\mu + \beta_1 * SVL_t)}}$
Size Dependent Fecundity	$Clutch\ Size = c + m * SVL_t$

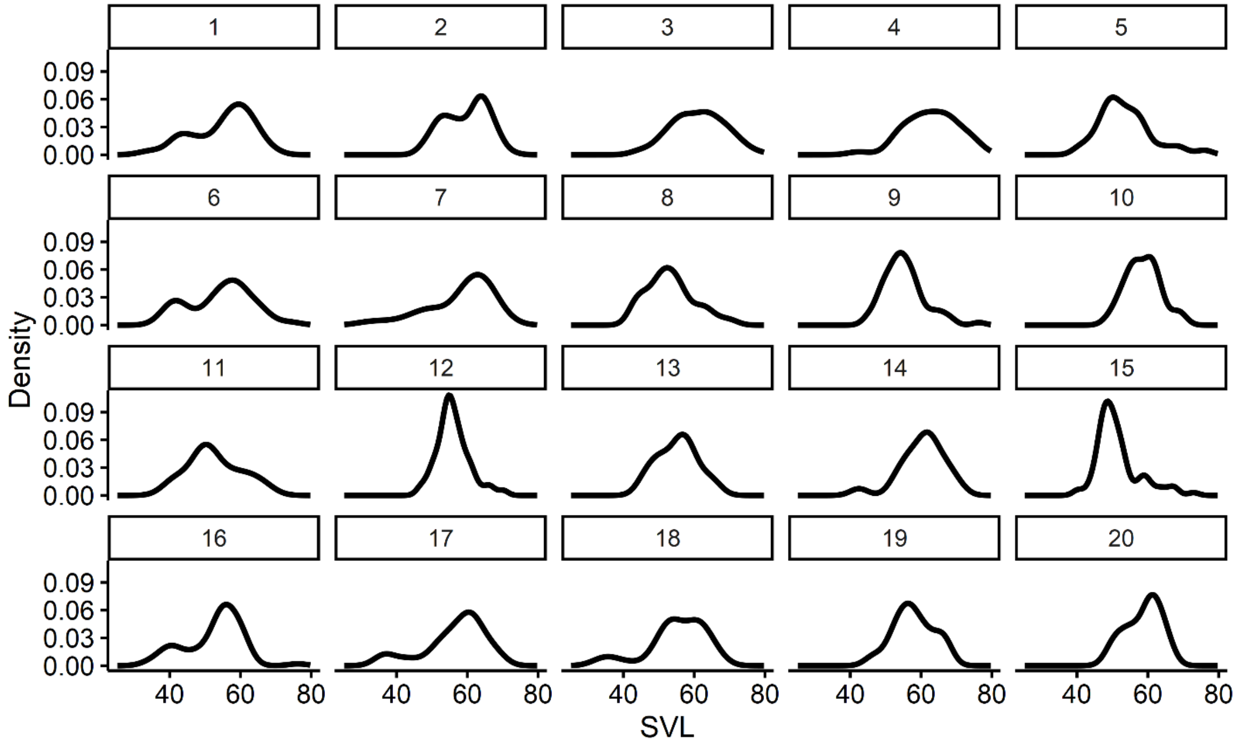

Figure S1. Smoothed size densities of Reticulated Flatwoods Salamander (*Ambystoma bishopi*) populations observed over 10 breeding seasons (2010–2020) at two populations on Eglin Air Force Base, Florida. Panels 1–10 are for Pond 4, and panels 11–20 are for Pond 5.

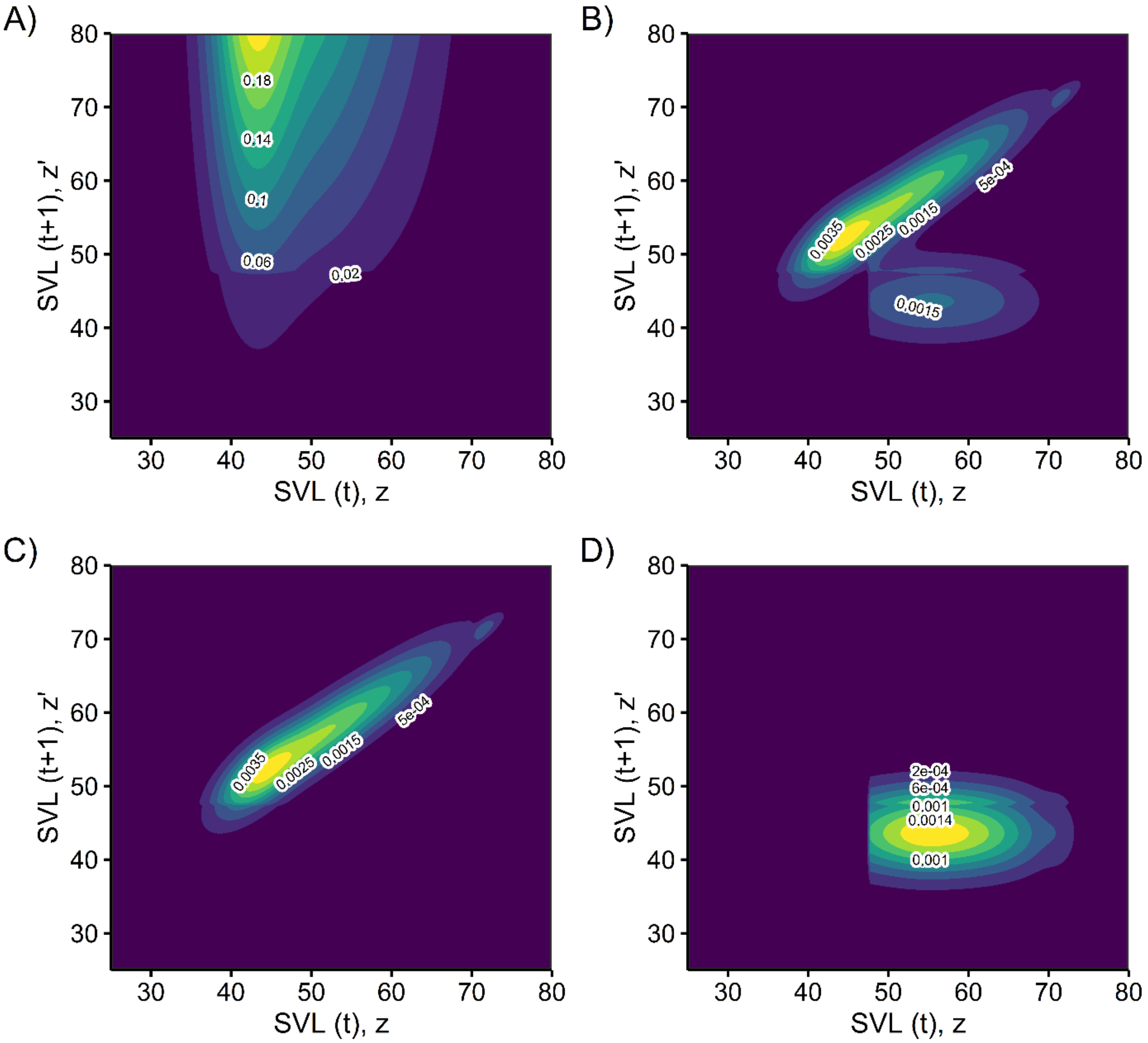

Figure S2. Sensitivity (A) and elasticity (B – combined kernel, C – survival kernel, D - fecundity kernel) analyses for an Integral Projection Model describing the population dynamics of Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) during long hydroperiod breeding seasons.

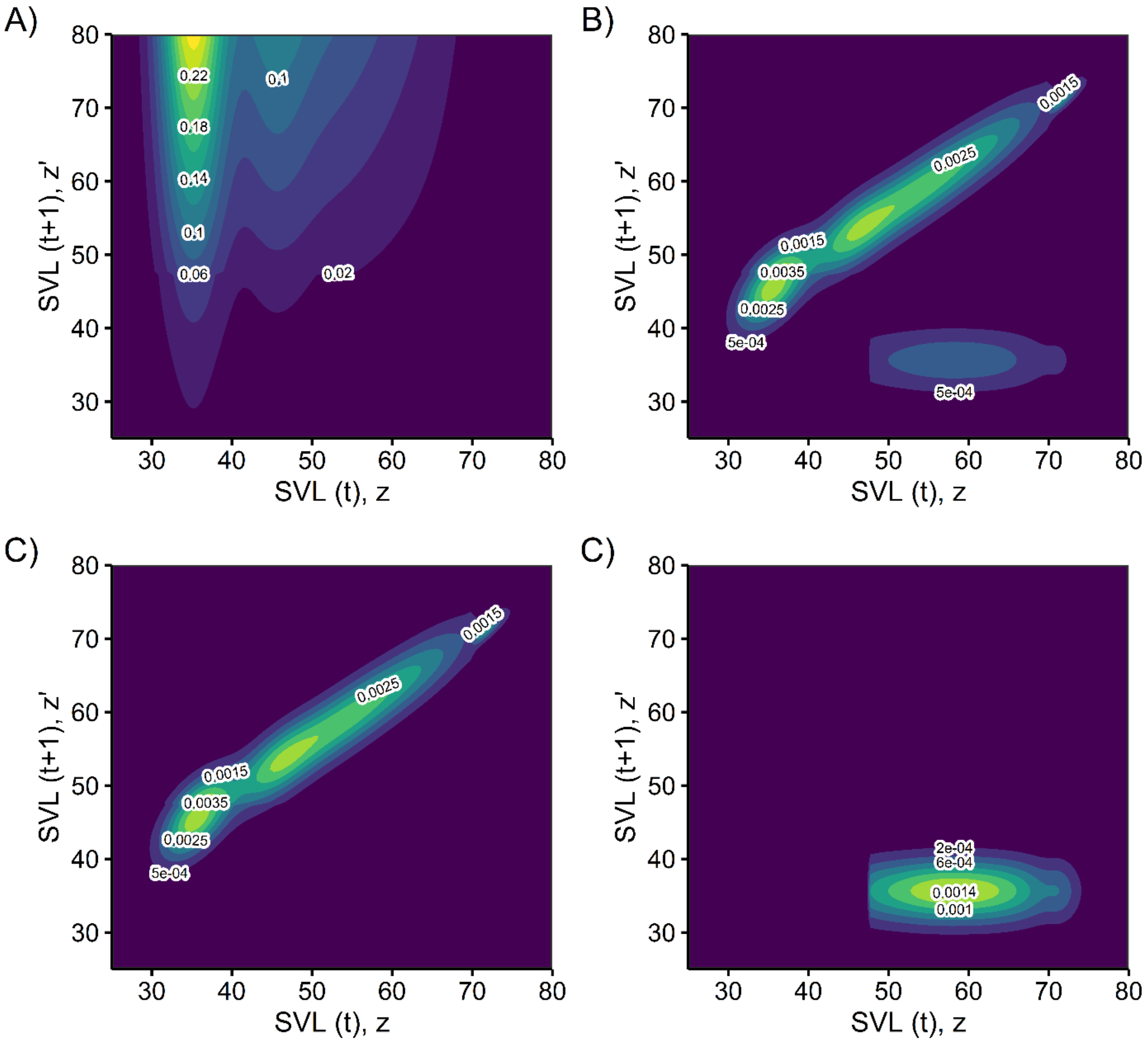

Figure S3. Sensitivity (A) and elasticity (B – combined kernel, C – survival kernel, D - fecundity kernel) analyses for an Integral Projection Model describing the population dynamics of Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) during short hydroperiod breeding seasons.

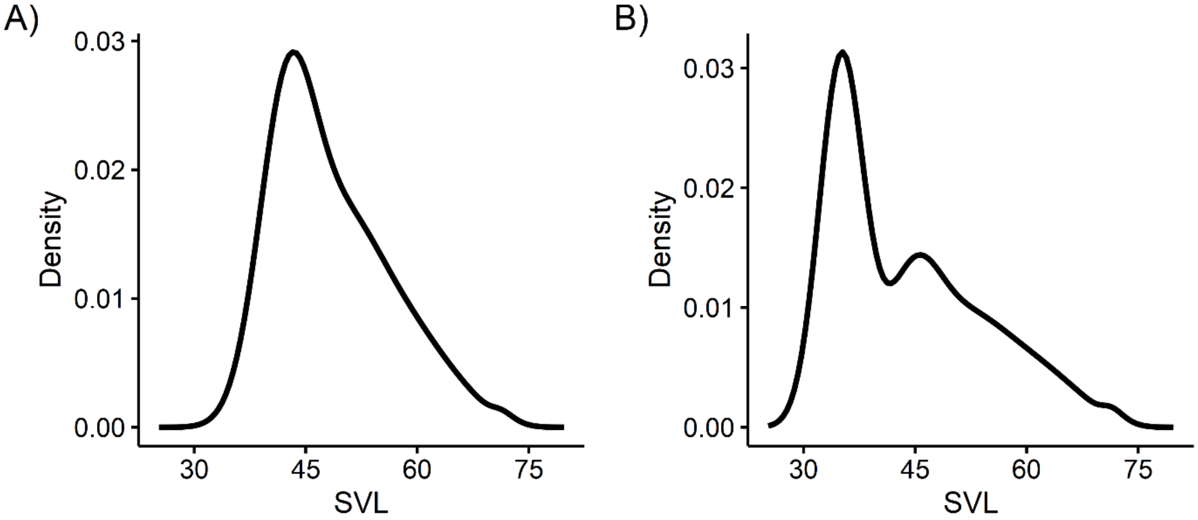

Figure S4. Stable size distributions from an Integral Projection Model describing the population dynamics of Reticulated Flatwoods Salamanders (*Ambystoma bishopi*). Models described reproduction occurring during both long (A) and short (B) hydroperiod breeding seasons, which impacted the size distribution of new recruits.

APPENDIX E

All material associated with Chapter 4. Additional details about indigo snake Integral Projection Model, including demographic equations, elasticity and sensitivity plots, and the stable size distribution.

Table S1. Equations describing demographic processes used to build an Integral Projection Model for Eastern Indigo Snakes (*Drymarchon couperi*). Parameter values are listed in Chapter 4: Table 1.

Process	Equation
Mean Individual Growth	$SVL_{t+1} = SVL_t + (L_\infty - SVL_t) * (1 - e^{-k*0.365})$
Growth with Individual Variation	$N(SVL_{t+1}, 0.03)$
Size Dependent Survival	$\frac{1}{1 + e^{-(\mu + \beta_1 * SVL_t + \beta_2 * (Road\ Density))}}$
Size Dependent Fecundity	$Clutch\ Size = c + m * SVL_t$

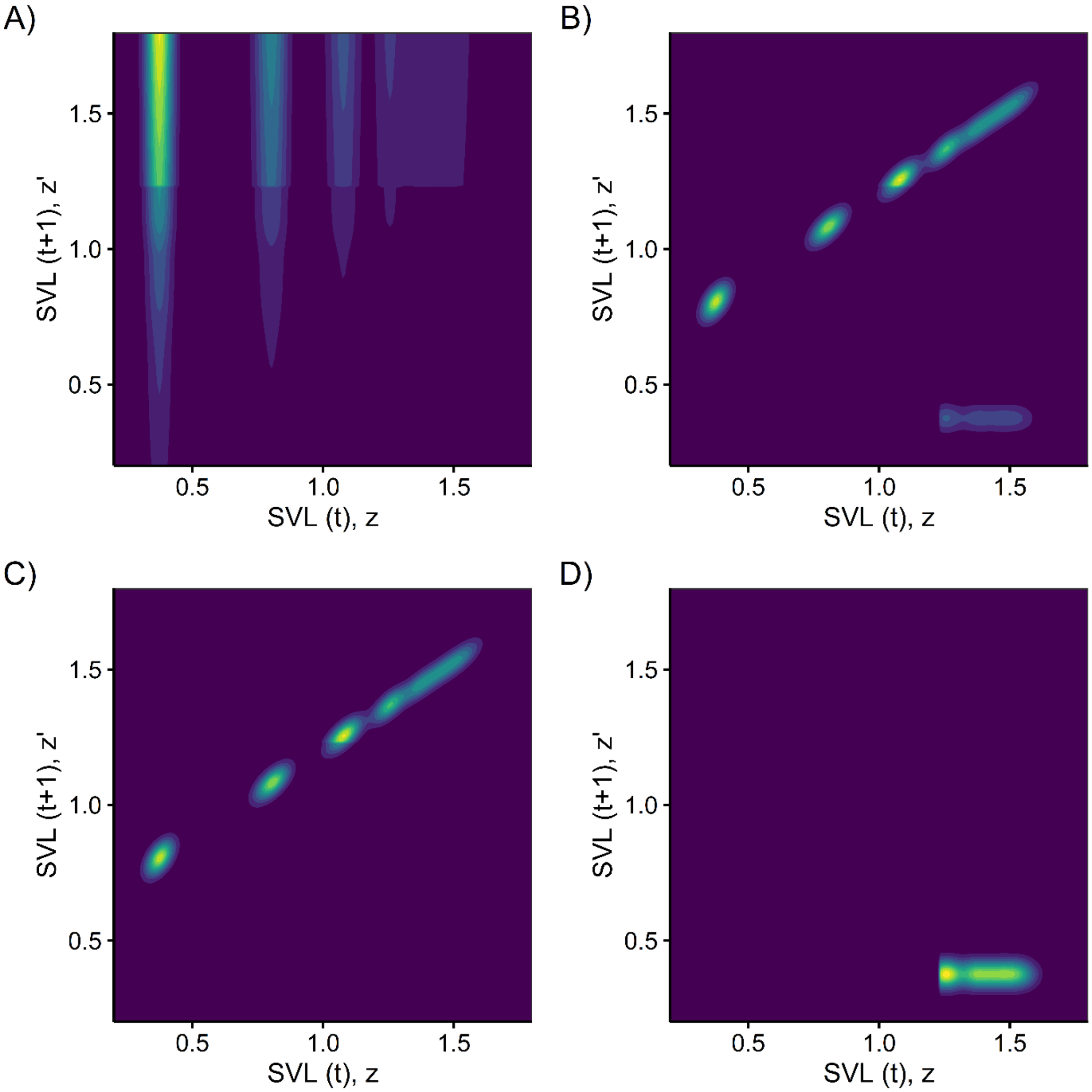

Figure S1. Sensitivity (A) and elasticity (B – combined kernel, C – survival kernel, D - fecundity kernel) analyses for an Integral Projection Model describing the population dynamics of Eastern Indigo Snakes (*Drymarchon couperi*).

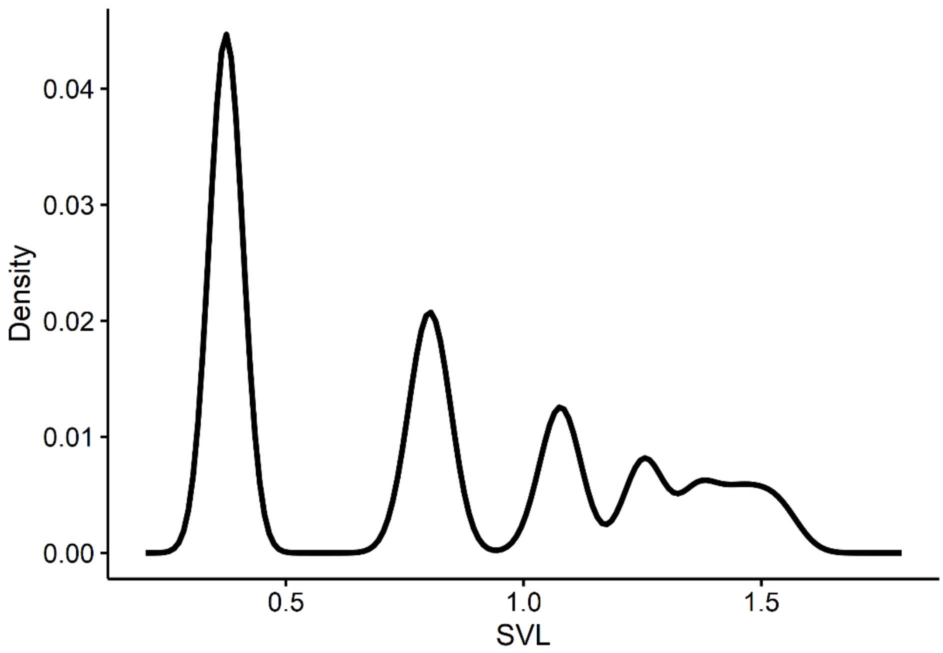

Figure S2. The stable size distribution from the mean kernel of a stochastic Integral Projection Model describing the population dynamics of Eastern Indigo Snakes (*Drymarchon couperi*).