CONSERVATION AMIDST COMPLEXITY:

STRATEGIC APPROACHES TO INFORMED DECISION-MAKING FOR MANAGEMENT OF A RARE ENDEMIC SALAMANDER

by

CORRIE J. NAVIS

(Under the Direction of John C. Maerz)

ABSTRACT

The conservation of rare and data-deficient species with highly complex and plastic life histories can present a particularly difficult challenge to wildlife managers. When data are limited but conservation status drives the need for prompt intervention, it can be difficult to weigh alternate management approaches and predict anticipated outcomes. In this dissertation I present multiple components of varied research to better understand and guide management decisions for the conservation of Striped Newts in the southeastern United States. In Chapter 2, I contextualize this research and situate it in place by examining the interconnected human and ecological histories of a tract currently managed for species conservation in southwestern Georgia. In Chapter 3, I use data from observational field research to fill gaps in knowledge on the dynamics of a Striped Newt population in Georgia. In Chapter 4 I use *ex situ* and *in situ* experiments to evaluate post-release outcomes of common captive rearing and repatriation strategies and reveal carryover effects of captivity on Striped Newt development after release. Chapters 5 and 7 address practical considerations related to captive husbandry of Striped Newts; Chapter

5 covers outcomes and lessons from a pilot experiment to reduce development consequences of captivity on Striped Newts through use of outdoor mesocosms, and in Chapter 7 I report the first protocol shown to eliminate *Batrachochytrium dendrobatidis* in infected captive Striped Newts. In Chapter 6 I combine results from other studies in this dissertation and other best available data to develop a population viability model with utility in guiding conservation decisions between alternate management strategies and in identifying priority areas for further research.

INDEX WORDS: *Notophthalmus perstriatus*, population viability analysis, captive breeding, repatriation, capture-mark-recapture, socioecological systems, natural history, complex life cycle, facultative paedomorphosis, phenotypic plasticity

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DEDICATION

Potok, Newt, Noah: I wouldn’t be here without you. Love you forever & always.

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Attempting to express my gratitude here for all of the individuals who have made this work possible and supported me along the way would likely take me another seven years, so suffice it to say that I owe my sincere thanks to countless people without whom this research would not be what it is (nor would I be who I am today).

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Captive breeding for conservation

Captive breeding is a common strategy in imperiled species conservation as a means of creating assurance colonies, managing genetic diversity, and facilitating repatriation or migration to suitable habitat (Griffiths and Pavajeau 2008, Comizzoli and Holt 2019). Such programs have seen much-heralded successes in the repatriation of highly endangered species that had been functionally extinct in the wild, such as the California Condor (*Gymnogyps californianus*) (Toone and Wallace 1994), Przewalski's horse (*Equus ferus przewalskii*) (Zhigang and Hao 2019), Española giant tortoise (*Chelonoidis hoodensis*) (Cayot 2020), and golden lion tamarin (*Leontopithecus rosalia*) (Kierulff et al. 2012), though overall the "success" of captive breeding and repatriation efforts has been mixed (Seddon and Armstrong 2016, Gross et al. 2024). Such reintroductions, even if considered successful in preventing extinction, often do not mean an end to necessary interventions for conservation purposes. Persistent and emerging threats in the species' native range often mean that additional management actions are needed in the long term to prevent further population declines (Seddon 1999, Scott et al. 2010, Turghan et al. 2022).

Frequently, reaching even short-term measures of success for a captive breeding and repatriation initiative can be a challenge, beginning with captive husbandry. Data on the characteristics of successful captive breeding and reintroduction methods are unfortunately scarce for most taxa (Mathews et al. 2005). Animals are often collected from the wild to establish captive breeding colonies when a species has substantially declined and is at imminent risk of extinction. This can result in the initiation of captive breeding programs without sufficient knowledge about the species' ecological needs and life history in the wild (Sarrazin and Barbault 1996, Tapley et al. 2015, 2024). While it is easier to provide for the needs of some animals than others, maintaining any species in captivity and managing a captive breeding program may be more costly than *in situ* conservation interventions (Bowkett 2009). Species maintained for a long time or multiple generations in captivity may be poorly adapted to their intended release locations due to changing environmental conditions within their native habitat, genetic adaptation to captivity, or unsuitable genetic representation among parental generations (Sarrazin and Barbault 1996, Araki et al. 2007, Bowkett 2009, Kleiman et al. 2010, Tapley et al. 2015, Crates et al. 2023, Gross et al. 2024). Mitigating those issues must be carefully considered when developing husbandry and breeding plans.

Once captive breeding programs have produced animals, post-release monitoring is critical to evaluating whether the initiative's objectives were achieved (Germano and Bishop 2009, Tapley et al. 2015, 2024). It is not possible to define universal measures of repatriation success that would apply to all animal species, due to widely varying life histories (Seddon 1999, Miller et al. 2014), though certain criteria are often applied. Commonly a repatriation attempt is considered a "success" if there is documentation of a progression of milestones: (1) post-release survival of captive-bred or -reared animals; (2) reproduction in the wild by released animals and successful recruitment of their offspring into the breeding population; and (3) projected persistence of the repatriated population, usually estimated via monitoring of vital rates or population dynamics to model population growth or persistence (Seddon 1999, Germano and Bishop 2009, Miller et al. 2014). A monitoring period of sufficient length for released animals and their offspring to have reached sexual maturity so those outcomes can be assessed is a minimum requirement for evaluating captive breeding and repatriation programs. For slow-maturing species, this post-release monitoring may require years or decades for reasonable evaluation (Miller et al. 2014, Canessa et al. 2016), but such monitoring is necessary to evaluating outcomes and adapting ongoing conservation approaches as needed (Germano and Bishop 2009, Tapley et al. 2024). Many repatriation programs—whether releasing captive-bred animals or translocated wild animals—do not report assessments of their success or failure, and the outcomes of many others remain uncertain (Miller et al. 2014, Resende et al. 2020).

Amphibian captive breeding and repatriation

Globally, amphibians represent the most imperiled class of vertebrates, with estimates ranging from 40 – 53% of species currently threatened with extinction (Della Togna et al. 2020). Amphibian declines in recent decades have heightened focus on amphibian conservation, including interest in the establishment of captive assurance and breeding colonies (Bowkett 2009, Scheele et al. 2019, Fisher et al. 2021). Due to relative ease of breeding in captivity and limited space demands relative to many vertebrate taxa, amphibians are generally considered good candidates for captive rearing and translocation efforts (Bloxam and Tonge 1995, Bowkett 2009). Both the number of captive breeding programs and the number of amphibian species maintained in captivity have substantially increased since the release of the first IUCN Amphibian Conservation

Action Plan in 2007, which identified captive programs as one of eleven key actions for amphibian conservation in the modern era (Della Togna et al. 2020).

Due to unresolved threats in their native habitats, for many amphibian species in captive breeding programs there exists no immediate plan for repatriation. The "ark paradigm" of conservation supports maintaining species in captive assurance colonies as a safeguard against their total extinction (Griffiths and Pavajeau 2008, Bowkett 2009, Tapley et al. 2015, Harding et al. 2016). Indefinite maintenance of captive amphibian colonies is not without costs and challenges. The up-front costs of establishing facilities suitable to house expanding breeding colonies, even for small amphibians with relatively limited space requirements, can still be substantial (Tapley et al. 2015). Amphibians' complex life histories require providing for the needs of multiple life stages with potentially quite different ecological niches, and failures to get captive conditions right can impact the fitness of animals both in captivity and post-release (Tapley et al. 2015). Captive breeding programs should be designed based on sufficient knowledge of the species' biology and ecology in the wild to ensure animals are suitable for eventual release to their native environment, but many still rely on trial-and-error and anecdote-based approaches to husbandry procedures (Tapley et al. 2015, 2024). Genetic adaptation to captivity is also of high concern for amphibians, some of which have short generation times and thus increased opportunity for selection against environmentally sensitive larvae over the course of multiple generations in captivity (Tapley et al. 2015).

Despite these challenges, numerous amphibian reintroductions have occurred in effort to reestablish extirpated populations or augment those in decline (e.g., Daly et al. 2011, Bodinof et al. 2012, Zhang et al. 2016, Rorabaugh et al. 2020, Thompson et al.

2022), with varying degrees of post-release monitoring and population impact. The outcomes of many herpetofauna releases remain uncertain due to limits of monitoring or species characteristics (e.g., long time to maturity) but broadly ~41% of such projects have been considered a success (Germano and Bishop 2009, Miller et al. 2014). Successful repatriation efforts tend to be published more often than failures or those for which outcomes remain uncertain, so available literature may present a disproportionately optimistic picture of captive breeding and release as a conservation solution (Miller et al. 2014). Despite these outstanding uncertainties regarding success rates—and the lack of clear frameworks for developing protocols likely to improve those chances of success—amphibian translocations (using captive-reared or wild-collected individuals) is often presented as a proven approach to imperiled species conservation (Seigel and Dodd 2002). Defining measures of repatriation success, analyzing the impact of captive-reared amphibian releases, and evaluating the projected population impact of alternate approaches are important components of continually improving the outcomes of such efforts (Dodd and Seigel 1991, Sarrazin and Barbault 1996, Seigel and Dodd 2002, Canessa et al. 2014, Kissel et al. 2014, Robert et al. 2015, Folt et al. 2020, Karlsdóttir et al. 2021).

Conservation of Striped Newts

Within the southeastern United States, Striped Newts (*Notophthalmus perstriatus*) are a species that may benefit from—or ultimately depend upon—captive breeding and repatriation efforts. Striped Newts are native to pine savannas of the North American Coastal Plain, which have declined by at least 95% over the past two centuries due to extensive logging, land use conversion, and fire suppression (Smith et al. 2000), resulting in little remaining suitable habitat for the species. Within these ecosystems, Striped Newts are dependent on isolated ephemeral wetlands for breeding. Such wetlands often lack regulatory protections, and many have been lost or degraded through ditching, draining, and fire suppression that has allowed the encroachment of pine and hardwood tree species. Striped Newts are presently a Species of Greatest Conservation Need (SGCN) and state-listed Threatened species in both Florida and Georgia, the only two states in their range on the Atlantic Coastal Plain (Georgia Department of Natural Resources 2017, Florida Fish and Wildlife Conservation Commission 2022). The species was previously petitioned for federal protection under the Endangered Species Act (ESA) (Means et al. 2008) and was initially deemed warranted for listing but precluded by higher-priority listing actions (U.S. Fish & Wildlife Service 2011). In 2018, however, the U.S. Fish & Wildlife Service declined to list Striped Newts under the ESA, citing the identification of additional populations since the initial petition (notably, the population central to the research presented here) and the high percentage of known Striped Newt populations that occur on publicly-managed land (U.S. Fish & Wildlife Service 2018). Environmental organizations have since accused the agency of employing quotas and similar policies to unjustifiably delist or deny species listings under the ESA—specifically citing the agency's reversal of its assessment of Striped Newts (Southern Environmental Law Center 2019)—and the Center for Biological Diversity recently filed a notice of intent to sue the U.S. Fish & Wildlife Service over the agency's final decision that Striped Newts were not warranted for ESA listing (Stewart-Fusek 2024).

Regardless of federal status, wildlife managers and researchers directly involved with the species believe that Striped Newts face a highly uncertain and precarious future.

Throughout their range, populations of Striped Newts appear to have disappeared or declined over recent decades such that few robust remaining breeding populations are known (Dodd and LaClaire 1995, Franz and Smith 1999, Farmer et al. 2017). While the majority of these indeed occur on publicly-managed lands, this is likely in large part an artifact of the challenges of identifying any populations of the species that are extant on privately owned lands (Means et al. 2008)—which in Georgia comprise over 90% of the state (Georgia Department of Natural Resources 2024). These known remnant Striped Newt populations are highly isolated from one another by vast expanses of intensive agriculture and other land development (Dodd and LaClaire 1995, Farmer et al. 2017), preventing natural recolonization or gene flow between locations, and at many extant sites rely on a single breeding wetland (Farmer et al. 2017). Captive breeding and release programs therefore may be vital to reestablishing Striped Newt populations in suitable remnant or restored breeding habitat or to bolstering population resilience by establishing additional breeding wetlands near a known Striped Newt pond.

A notable hurdle in the captive rearing of Striped Newts for release is the species' highly complex life history. The species develops along the life history cycle typical of newts (Family Salamandridae, Subfamily Pleurodelinae) (Figure 1.1). Eggs are individually attached to submerged aquatic vegetation, and hatch into aquatic larvae. After a period of larval growth, one of several partial or fully metamorphic pathways are possible. The most well-known—but not necessarily the most common—pathway is that larvae metamorphose into a terrestrial, juvenile eft stage within the first year of life, then emigrate to terrestrial habitat and remain in that juvenile life stage, growing slowly for up to several years before reaching maturity and returning to wetlands to reproduce (Johnson

2003, 2005). Striped Newts are also facultatively paedomorphic: if a wetland retains water beyond the larval period, larvae will undergo partial metamorphosis while retaining some neotenic characteristics—most notably external gills. These paedomorphic forms are thus obligately aquatic, and typically reach reproductive maturity within a year of hatching. Such paedomorphs are a common developmental outcome in at least some Striped Newt populations (Mecham 1967, Johnson 2005; see Chapter 3). Paedomorphic adults can eventually complete metamorphosis and lose their gills. The precise suite of triggers for the different developmental pathways are not fully known, but in other facultatively paedomorphic salamanders (including other newt species), the proximate triggers of alternative life history pathways include wetland hydroperiod, temperature, resource competition, and other density-dependent processes (Newman 1992, Denoël et al. 2005).

Many Striped Newt life stages are not conducive to *in situ* study and so our understanding of their life history and population dynamics is relatively limited (Means et al. 2008, Burton et al. 2012). Little is known about the vital rates of most life stages and how they influence population growth and dynamics (Means et al. 2008; Burton et al. 2012). Some researchers have characterized development into terrestrial forms (i.e., larvae transitioning into efts and any paedomorphs automatically transitioning into fully metamorphic adults) as being the predominant life history pathway in Striped Newts (Johnson 2001, Dodd et al. 2005), in which case terrestrial survival would be important to population dynamics. However, other studies suggest that partial metamorphosis to a rapidly breeding paedomorphic adult might be the “default” ontogenetic pathway under suitable wetland conditions (Johnson 2005), giving Striped Newts the capacity for rapid population growth following wetland drying or drought events. In other words, the paedomorphic pathway might be the engine of population growth, while terrestrial stages are the storage phases that ensure population persistence through periods of reproductive failure and drought. These characterizations of Striped Newt life histories—while sometimes asserted with certainty—are untested hypotheses that need deeper thought and to be confronted by data.

A number of entities (e.g., zoos and other non-governmental organizations) in and beyond the southeastern U.S. are engaged in captive breeding of Striped Newts for repatriation to historic breeding ponds or supplementation of existing populations, with a focus on increasing captive rearing capacity to produce additional newts for release each year (Means et al. 2017). However, such releases are somewhat opportunistic, with often little information or consideration of what life stages are most effective targets for captive rearing and release programs, how best to raise newts to target life stages, when to release newts to optimize post-release success, and where to collect or release newts to meet conservation objectives. In practice, most actions are opportunistic based primarily on project limitations (e.g., limits to resources an organization is able to devote to rearing larvae or greater numbers of breeding pairs) or environmental constraints (e.g., the need to release larvae before ephemeral wetlands dry annually) (Means et al. 2011). There have so far been no rigorous assessments of the outcomes for released Striped Newt larvae or any determination of whether targeting later stage larvae, metamorphosed juveniles, or adults would be more effective in recovering populations.

Objectives

The objectives of this dissertation are to (1) estimate vital rates of Striped Newts at Sandhills Wildlife Management Area (SWMA) in western Georgia, (2) use a combination of *ex situ* and *in situ* studies to understand the likelihood of developmental pathways differing between captive and wild populations, and (3) develop a population model for Striped Newts that can inform management decisions.

Before delving into my research on the ecology and natural history of Striped Newts, I begin in Chapter 2 with an exploration of the socio-ecological histories of land that today is set aside as SWMA and managed for conservation of Striped Newts and other imperiled species. Seldom are such conservation lands "pristine," undisturbed wilderness. More often, they are landscapes that have been shaped by both natural processes and human activities. Further, the meaning and importance of those spaces can vary among local communities. I make a case for the importance of understanding the context of places and communities where biodiversity conservation work is carried out.

In Chapter 3, I present the results of a more than two-year field study of the Striped Newt population at SWMA, which represents a rare opportunity for research on population dynamics within the declining western genetic sub-group of Striped Newts. The population data resulting from this research adds to knowledge about the complexities of Striped Newt life histories and informs other parts of this research.

In Chapter 4, I evaluate post-release survival and developmental outcomes for larval Striped Newts reared under common husbandry practices for the species, using soft-release enclosures to improve detectability for post-release monitoring. The results of this research are the first published study tracking captive-reared Striped Newts after release to document outcomes and identify potential tradeoffs in survival and developmental consequences of larval size at release.

Chapter 5 presents the results of an outdoor mesocosm captive rearing experiment, piloted to address some of the conditions of captivity that may result in undesired developmental effects on larval Striped Newts.

In Chapter 6 I synthesize data from my research and vital rates available in the literature and create the first population projection model for Striped Newts, facilitating comparison of alternative captive rearing and release strategies for repatriation and population management. The intention of developing this model is to provide a practical tool to inform decisions by Striped Newt captive rearing and repatriation programs in Georgia and Florida.

Chapter 7 presents a treatment protocol I employed to successfully clear our captive Striped Newt breeding colony of incidental *Batracochytrium dendrobatidis* infection.

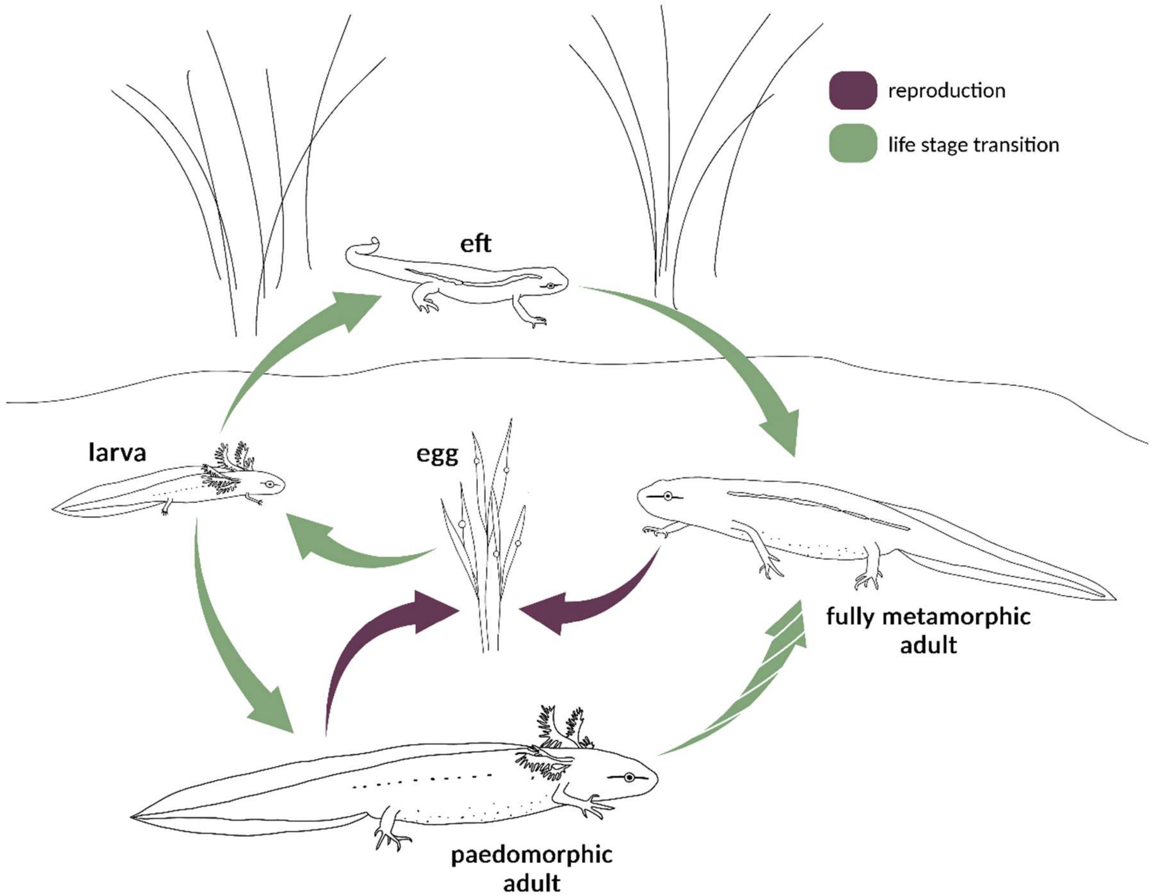

Figure 1.1. Striped Newt life cycle. Transition from paedomorphic to fully metamorphic adult is shown with a dashed arrow, as while some have suggested it occurs after the first breeding season as a paedomorph (even if the wetland does not dry), tendency to complete metamorphosis likely varies among populations; in our field research we have seen no evidence that it occurs as a matter of course when wetland conditions allow newts to remain in gilled aquatic forms. Fully metamorphic adults may move between terrestrial and aquatic environments and often undergo temporary physiological changes associated with that habitat transition or with the onset of the annual breeding season, but these are reversible (and vary by sex), and we do not consider their use of the two environments to represent distinct life stages.

CHAPTER 2

CONSERVATION IN CONTEXT: A CASE STUDY FROM RURAL GEORGIA, U.S., HIGHLIGHTS THE RELEVANCE OF SOCIOECOLOGICAL HISTORIES OF PLACE[1]

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Abstract

The interconnected social and ecological histories of particular places provide context for understanding the formation of current ecosystem states; trends in land-use dynamics; community perspectives on “wild” spaces, land ownership, and control of land; and ways in which community members have developed varying relationships towards “natural” spaces. I provide an overview of influential aspects of the social histories and ecological changes that have shaped a particular tract of land now set aside for biodiversity conservation in rural southwestern Georgia, U.S. Through highlighting the ways in which these histories provide important context to the relationships between humans and the landscape in this region, I hope to illuminate the value of applying similar consideration of socioecological context when undertaking management of any place for conservation purposes.

Introduction

Much has been written by natural and social scientists regarding the role of land in conservation: the function of green spaces in public life, the “fortress” model of conservation, and the social processes that underlie how humans use “natural” spaces. There is also value, however, in understanding the unique socio-ecological history and context of a particular place that has been set aside for conservation purposes. Understanding a place’s ecological history is a concept well embraced in the field of restoration ecology: humans impact the landscapes where we live, and even the relatively distant human past may have shaped the ecosystems we today take for granted as “natural” assemblages of plant and animal life (Pickett and McDonnell 1993, Szabó 2010, Coughlan and Nelson 2018). A certain historical condition (or range of conditions) is often selected as a "reference" ecosystem to serve as a target when undertaking ecosystem restoration initiatives (Balée 1998, Szabó 2010, Higgs et al. 2014). Understanding the ways humans contributed to the state of both degraded and reference ecosystems is an important factor in planning to achieve conservation objectives (Bürgi and Russell 2001, Balée 2006, Szabó 2010).

That linked socio-ecological past is also relevant to individuals' and communities' sense of place, which can in turn influence local environmental concern and place-protective behavior (Brehm et al. 2013), and to justice issues tied to the landscape. Abiotic and biotic features of a landscape influence societies' use of a place, their ties to it, and the environmental values they associate with it (Glassberg 2001, Choy et al. 2010, Higgs et al. 2014). Those connections to place may vary greatly between individuals or societal groups and may not always be positive associations. For example, "wild" marginal spaces often held a quite different place in the perspectives of slavery-era white, Black, and Indigenous residents of the U.S. South (Finney 2014, Armstrong 2017, Heynen and Ybarra 2021). Perceptions of both particular locations and types of place (e.g., undeveloped landscapes) are thus not universal or inherent but are shaped by past experiences, often passed down in communities across generations (Johnson and Bowker 2004). Understanding the complexities of such socio-ecological histories can inform conducting conservation work in a socially just manner (Armstrong and Veteto 2015).

Focusing socio-ecological investigations on the scale of a discrete place can reveal the ways it has been (and continues to be) influenced by both local and global social forces (Biersack 2006) and is unlike any other plot of land in the world (Szabó 2010). Similar explorations of the history of particular locations have provided depth of insight into the social and environmental conditions of the present day, e.g., Pulido's (2000) examination of historical social change and inequity of environmental risk in the Los Angeles area.

My interest in exploring the interconnected human and ecological histories of place was sparked by a rather different landscape than industrial city cores. The Fall Line Sandhills Region of Georgia is a region of exceptionally high biodiversity, including high richness of amphibians and reptiles (Wharton 1989, Graham et al. 2010). In 2007 the Georgia Department of Natural Resources purchased a parcel of land in this region to expand Sandhills Wildlife Management Area (SWMA) in Taylor County, Georgia, U.S. for conservation of rare plant and animal species found to persist there (Georgia Department of Natural Resources 2021). SWMA consists of two disjunct tracts totaling nearly 640 ha; the east tract, located just northwest of the town of Butler, comprises just over a quarter of that area. It was while conducting ecological field research on Striped Newts (*Notophthalmus perstriatus*) in “Big Pond” on the east tract that I became curious about the present and historical societal dynamics on and surrounding the property. SWMA east was previously a commercial timber property, and it has a long history of other uses before being set aside for biodiversity conservation. Those shifting uses over time—and its place today as a relatively small tract of conservation land, surrounded by privately owned property and commercial enterprises—are important parts of its context that I wished to explore.

The aim of this paper is to illuminate some of that socio-ecological history of the piece of land now managed as SWMA East—particularly during periods of the greatest changes that shaped the landscape and how residents related to it—and how that history of human-nature relations may impact ongoing perceptions of and interaction with the land under its current designation and management. I further hope to highlight the relevance of applying similar consideration of socio-ecological history and context to any place being managed for conservation purposes.

For simplicity, I hereafter reference the east tract solely as SWMA, although it was not designated as such until quite recently (similarly, I generally reference other geographic places by their modern names). Though the west tract is not the focus here, many of the regional circumstances discussed may similarly relate to both portions of the managed property.

Approach

I included a broad range of source material in my search, from academic articles and books to contemporary newspapers, published journals, government records, maps and photographs. Piecing together a reasonably complete history can be challenging as there exists little written documentation of life in the region prior to ca. 1800 (Szabó and Hédl 2011) and even in periods when such records were more common, the lives of marginalized societal groups continued to be largely underrepresented in surviving materials (Johnson 2017). Many existing historical records discuss broad processes or cannot be easily linked to a known present-day location due to imprecise or changing place names. In seeking to unravel this history of place, I aimed to uncover reports of life as local as possible to the area around SWMA, but the area has not received a great deal of focus in historical accounts. Today the town of Butler, GA is home to just over 2,000 residents, with fewer than 8,000 in all of Taylor County (U.S. Census Bureau 2020a, 2020b). Far more has been published about historical conditions and events in more populated nearby areas, such as the city of Columbus (approximately 65 km WSW of SWMA). However, it is possible to situate available details about a particular place within those better-documented social and ecological changes occurring in the broader region over time. Places are influenced by both local and global social forces (Biersack 2006), and integrating multiple ways of knowing about the histories of a place can result in a more complete understanding of it (Szabó 2010).

I planned to supplement available published information from recent periods by conducting anonymized, semi-structured interviews of individuals with insight into the land's recent history and community perspectives on its present status as a state-managed conservation property. My aim was to use "snowball sampling" to obtain further recommendations of contacts to interview, an approach that requires some flexibility but can useful in identifying additional parties who could augment a narrative (Moser and Korstjens 2018). However, limited response from invited interviewees prevented that effort from gaining traction. I was able to conduct a semi-structured interview with one participant who has insight into the recent history and management of the land, and whose comments are referenced in this paper as Interview 1.[2]

A Brief History of Place

Pre-human ecology

SWMA is located along what today is known as the Fall Line—the geologic boundary that cuts across the state and is considered the dividing line between north/central and south Georgia. The elevational change between the piedmont north of

[2] Interview conducted 18 August 2024 by C. Navis. Semi-structured interview guide provided in Appendix I.

the Fall Line and the North American Coastal Plain to the south exists due to planetary changes that occurred long before humans inhabited the planet, let alone this region. The Coastal Plain formed during the Cretaceous Period (~165 – 45 mya), which was characterized by a great deal of tectonic and climatic change, with widely fluctuating sea levels (Gale 2000, Miller et al. 2004). During this period, sediments carried by rivers and streams, wave erosion of shoreline substrates, and deposition of marine minerals and organic materials such as chalk combined to gradually build up layers of material atop the continental shelf (which extends some distance beyond the modern-day coastline) (Stephenson 1926, Gale 2000). What we know today as the Coastal Plain of south Georgia has likely only been consistently exposed above sea level since the mid-Pliocene epoch (~3.3 – 2.9 mya) (Rovere et al. 2015).

The Cretaceous deposits that make up the sands and clay soils of the Fall Line Sandhills physiographic regions represent the oldest portions of the Coastal Plain formation in Georgia, where sediments were first deposited off ancient shorelines (Wharton 1978). While similar sandhills environment can be found along the Fall Line in some eastern parts of the state, the best-developed Cretaceous dunes are represented in Talbot County and Taylor County, where SWMA is located; it is likely that this region is where the distinctive floral and faunal assemblages now representative of south Georgia first developed (Wharton 1978).

The Coastal Plain, once formed and exposed, continued to undergo additional pre-historic ecological changes. Paleobiological records indicate that from ~35,000 – 11,000 ya, changing climates and water levels contributed to periods of varied dominant forest assemblages across south Georgia; megafauna such as mammoths, mastodons, ground sloths, and bison persisted in the state throughout this time (Wharton 1978). These mammal species are believed to have been extirpated from the region by ~11,000 – 10,000 ya due to climate change at the end of the Wisconsin glaciation and hunting pressures from the first human communities to reach the southeastern parts of the continent (Wharton 1978). While paleoarchaeological estimates vary, evidence from sites in South Carolina and Florida point to human settlement of the region by 14,400 ya (Goebel et al. 2008).

Pre-historic human era

The earliest human residents of the southeast left no written histories, and what can be known of their lives and cultures must be inferred from paleoarchaeological investigation. I do not delve deeply into that branch of scholarship here, as the lives of more recent Indigenous peoples of the region are a degree better documented and more relevant to the recent contexts of this place. However, paleobiological and geological research provide insight into the world those early residents inhabited on the Coastal Plain.

By ~9,000 ya, scrubby oak forests with savannas of bluestem prairie grasses and sagebrush covered parts of south Georgia (although such records exist from areas of unique underlying geology, making it difficult to infer if similar ecosystems likely dominated other portions of the Coastal Plain as well) (Wharton 1989). The modern Coastal Plain ecological assemblages began forming ~5,000 ya, when rising ocean levels contributed to corresponding rise in groundwater tables; by 4,000 ya longleaf pine (*Pinus palustris*) savannas were the dominant upland forests across south Georgia, with cypress swamps forming in lowland areas (Wharton 1989).

Recent Native residents & European colonization

It can be challenging to gain reliable insight into the lives of Native[3] peoples prior to the arrival of European explorers and settlers in North America. Most nations did not have a written language (although a Cherokee syllabary was introduced in 1821; Cushman 2011), and the primary written accounts detailing Native societies during the early post-contact era come from white observers. As such, much is undoubtedly left out of these historical accounts; however, they can shed light on social and political events of the period and in some cases include information and perspectives recounted to the writer by Native individuals. They are also at times revealing about the writers' perspectives on the Indigenous peoples they encountered.

The Muscogee (Creek) people were the primary inhabitants of much of what is now Georgia when Europeans first arrived on the continent. They were not of a single nation, but represented a confederacy of related and allied groups across the region (Woodward 1859, Southerland and Brown 1989, Stiggins 2001, Hawkins and Foster 2003); over the eighteenth century, these peoples strengthened alliances and began to identify more strongly as a single nation as they resisted white encroachment on their homelands (Hudson 2010). Muscogee (Creek) traditions tell of their people's origins in lands west of the Mississippi River, but by the early 1700s they resided from the Mobile River to east of the Savannah River, north to Cherokee lands (by that time extending into north Georgia) and south to the Gulf Coast (Harrold 1939, Hemperley 1973, Hawkins and Foster 2003). Retreating from the eastern portions of their homelands as white

[3] See Appendix II for a note on terms and group names used in this paper.

settlement increased, western portions of Georgia and eastern Alabama remained strongholds of Muscogee (Creek) society (Figure 2.1).

Diaries and accounts by white writers during the 1700s describe a well-organized and powerful society. Thirty-seven main cities of the Muscogee (Creek) confederacy were organized along the rivers of west Georgia and Alabama, often comprising several smaller settlements and cultivated agricultural lands surrounding a primary city that was central to the activities of community life (Hawkins and Foster 2003). Each town had its own government, with established political processes for deciding issues ranging from war and peace to marriage and divorce (Hawkins and Foster 2003). Cultural celebrations and festivals marked significant seasons and might last over days of songs, dances, and rituals in larger cities (Stiggins 2001, Hawkins and Foster 2003). Travel was important in both Muscogee (Creek) mythology and in daily life; they established numerous paths between towns, often following landscape features such as rivers or ridges, and marked routes with hatches on tree trunks (Hudson 2010). While communities engaged in farming, hunting was also an important part of their subsistence, and in fall and winter most—other than the very young or elderly—largely left the cities to take to the forests for the primary hunting season (Hudson 2010). Not passive inhabitants of their environment, they and other southeastern Native peoples had for millennia shaped the longleaf-wiregrass savannas that once stretched over 37 million hectares of the Coastal Plain, employing fire to flush game, prepare land for agricultural cultivation, manage habitat for game species, and clear routes for travel (Shields 2008, Zhang et al. 2010, Stambaugh et al. 2011, Hanberry et al. 2023).

European settlers in Georgia increased in number beginning in 1733, the year after the Georgia Trustees (led by James Edward Oglethorpe) secured a royal charter from the British Crown to govern the region between the Savannah and Altamaha Rivers—an area hotly contested by the colonial powers of England and Spain over the prior 60 years (Jennison 2012). At the start of this formal arrangement, the trustees made the unusual decision to prohibit slavery in the Georgia colony—not on moral grounds, but fearing the threat of violent revolts that might destabilize the burgeoning colony (Jennison 2012). Within less than a decade of the colony's founding its economy had failed to gain a foothold and many residents departed for nearby colonies. The trustees gave in to pressure from colonists who wished to end the prohibition on slaves in Georgia, and the ban was lifted at the start of 1751 (Jennison 2012). The following year, the trustees' charter to oversee colonial Georgia expired, reverting governance to the British Crown.

The Crown soon implemented changes to land tract size limits and inheritance laws, setting the stage for the accrual of large plantations—and the labor required to make them profitable—that would shape the history of the colony and later, the state (Jennison 2012). These changes brought a new surge of colonists eager to try their chances in Georgia, with the colony's white population quickly ballooning from just 500 in 1741 to 18,000 by 1773 (Jennison 2012). The enslaved Black population grew just as quickly under the newly-legal system of slavery, as small transports of enslaved laborers from the West Indies were gradually eclipsed by shipments of hundreds of enslaved persons directly from Africa; the Georgia colony's Black population grew from just 600 in 1751 to 15,000 by 1775 (Jennison 2012). At the same time, governing bodies established for the colony were structured to privilege wealthy landowners—the same men who were capitalizing on the economies of scale that plantations and enslaved labor permitted. Over the final decades of Georgia's tenure as a British colony, they passed a series of slave codes that were a distinct departure from the 1750 code, which had put some restrictions on white residents' import of and treatment of enslaved Black persons; the new codes instead set increasing restrictions on Black life and agency, and outlined severe punishments for a range of infractions (Jennison 2012).

The antebellum United States

By the late 1700s, white settlers had not much encroached into western portions of Georgia, and no battles of the Revolutionary War extended beyond eastern portions of colony. In the decades following the nation's founding, however, a great deal of change came to western Georgia.

A Muscogee (Creek) trading path that traced the Fall Line across much of the state eased access into Creek territories for explorers documenting conditions of the newly formed country. In 1775, the noted naturalist William Bartram set out from Augusta on the latest leg of his southeastern journeys, following that path west across the state (Bartram 1791). Bartram documented his party's fording of the Flint River on July 5th and described the place where they made camp early that evening on a creek to the west: undulating land characterized by forests of massive timber, stands of tall cane (*Arundinaria* spp.), savannas providing quality grazing for the group's horses, and "innumerous" rivulets and streams draining into the Flint watershed (Bartram 1791). While there is no way to know the precise location of the party's camp that night, it would have been near the area of SWMA, which is ~22 km (13.7 mi) west of the Flint

River—directly on the path that Bartram and his team traveled. Bartram’s accounts of the following two days depict similar landscapes: rolling hills, open forests of pines standing over “expansive” savannas and streams, abundant flowering plants, and meadows of cane (Bartram 1791). Benjamin Hawkins, appointed in 1796 as the U.S. Agent for Indian Affairs South of the Ohio River, described the area similarly at the end of the decade. Upon his appointment he established his home and the new Creek Agency just east of the Flint River, along the old trading path, and wrote of rolling hills and rich swamps along the river’s shores (Hawkins and Foster 2003, Hudson 2010). It appears he held a somewhat less favorable view of typical south Georgia ecosystems, describing lands further south and those west of the Flint as being “poor,” dominated by pine forests with savannas of wiregrass and saw palmetto, dotted with ephemeral swamps that held water seasonally (Hawkins and Foster 2003).

Hawkins’s place became a popular stopping point for white travelers on the trading path route, though they were few in number at the start of the nineteenth century (Hawkins and Foster 2003). By 1806, it was used by horseback postal carriers traveling across the south (Southerland and Brown 1989, Hudson 2010). Meanwhile, a series of treaties had pushed back the eastern edge of Muscogee (Creek) territories: a tract west of the Oconee River was ceded in 1802, and lands west to the Ocmulgee River in 1805 (Hudson 2010). White travelers along the old trading path—now postal route—across the south and through Muscogee (Creek) lands were thus far limited by the difficult terrain and lack of development, describing the challenges of scaling bluffs, navigating swamps, and the trials of the dangerous “wilds” (Hudson 2010). In contrast, the route at times allowed a temporary degree of freedom for enslaved Black travelers, sent ahead as scouts to investigate the route for their enslavers (Hudson 2010).

In 1811 Hawkins brought the idea of expanding the path into a road for military use to a council of representatives from various nations in the Muscogee (Creek) confederacy. When they rejected this proposal, he told them that he was there to inform them of the plans already underway, not to ask their permission (Southerland and Brown 1989). By the end of the year the modifications had been made, ensuring that troops and equipment could be moved to expanding territories further to the west; at this juncture, it became known as the Federal Road (Southerland and Brown 1989, Hudson 2010). While part of the impetus for establishing clear routes through the South was to limit the travel of white settlers to certain courses through Native lands, this increase in military use and general travel of U.S. settlers along this route through Muscogee (Creek) lands resulted in correspondingly greater conflict (Southerland and Brown 1989, Hudson 2010). In the early decades of the 1800s, settlers eager to take advantage of lands in the "Old Southwest" (what would later become the state of Alabama) poured over the road in great numbers, despite the challenges of the terrain. In 1800, the U.S. populace in Alabama numbered only 1,250; by 1940, it has swelled to nearly 600,000 (Southerland and Brown 1989). A great many of those settlers traveled by way of the Federal Road through Muscogee (Creek) territory.

The council of Muscogee (Creek) leaders had good reason to be wary of expanded military and settler access through what remained of their homelands. Building roads was seen by many in the imperial enterprise as an important first step to spreading white settlers across the continent, cultivating the land and deriving economic profits from it (Hudson 2010). The Muscogee (Creek) came to dub white surveyors and speculators traveling in their territory ecunnaunuxulgee (those greedily grasping after our lands) (Hudson 2010). While they had welcomed exchanges with early white traders in the region, settlers attempting to claim ownership of their lands presented more of a problem (Hawkins and Foster 2003, Hudson 2010). Tensions increased as white settlers increasingly encroached upon Muscogee (Creek) lands and travelers along the Federal Roads were occasionally attacked. Such incidents culminated in the Creek War of 1813-1814, in which the confederacy was divided among those resisting U.S. expansion and factions throwing in their lot with the militarily powers of the colonizing nation (Southerland and Brown 1989). Numerous battles each left hundreds of Muscogee (Creek) fighters dead, and that winter saw many fleeing their cities to take refuge in swamps and forests, their crops destroyed and fearing the violence of U.S. military forces (Southerland and Brown 1989). The conflict officially came to an end with the Treaty of Fort Jackson in August 1814, in which the Muscogee (Creek) were forced to cede more than 8.9 million ha (22 million acres) of their remaining territory to the U.S. (Southerland and Brown 1989).

Travel by white settlers—and the enslaved Black people trafficked as they moved further west—resumed after the formal end of the Creek War (Southerland and Brown 1989, Hudson 2010). The sandy soils along the Fall Line continued to make Federal Road travel difficult; horse and wagon travel contributed to erosion until in many sections the road cut well below the surrounding ground level (Southerland and Brown 1989). Settlement and commerce persisted despite these obstacles. Even while most mail was carried from east coast cities to New Orleans via the longer (but better maintained)

Natchez Trace route through Tennessee, by ca. 1818 numerous post offices were popping up along the federal road, as well as many Christian churches (Southerland and Brown 1989). The Muscogee (Creek) confederacy, easily the most numerous residents of the area at the start of the century, by 1825 saw their 20,600 people well outnumbered by white settlers who continued to flood through and into their lands (Southerland and Brown 1989).

That year, General William McIntosh, of Muscogee (Creek) and Scottish heritage, signed the second Treaty of Indian Springs on behalf of the Muscogee (Creek) confederacy—which he did not have authority to represent (Southerland and Brown 1989, Hudson 2010). The treaty was modified slightly by subsequent versions over the next two years, but the end result was the Muscogee (Creek) ceding all of their lands between the Flint and Chattahoochee Rivers in western Georgia (Southerland and Brown 1989).

Meanwhile, the challenges posed by travel on the Federal Road were somewhat eased by the establishment of stagecoach lines, which by 1826 ran from Milledgeville (then the Georgia capital) to Columbus or Montgomery (Southerland and Brown 1989). The land lottery of 1827 distributed parcels of land in the newly available areas of western Georgia to "fortunate drawers," each entitled to lay claim to a tract of ~82 ha (~202 acres) (Houston 1929, Weiman 1991). Official opening of west Georgia to white residents brought a new flood of settlement into the region; often those moving to develop lands there were not those selected in a land lottery, but speculators who'd purchased lots from them (Weiman 1991). High demand for enslaved labor to extract profit from these newly-white-settled lands contributed to untold thousands of enslaved

Black people being “sold down the river,” transported from other slave states or involuntarily migrating to the region as their enslavers sought to capitalize on the newly available territory (Carey 2011). While these migrations of white settlers flowing across the antebellum South might suggest a lack of attachment to place, many sought to recreate and replant their culture, community, and family ties as they moved in search of new opportunity (Sherrod 2011). Rather than define themselves by place, they sought to reshape places to reflect what they valued.

Soon, even more lands would be available for settlers to shape. In 1830, U.S. President Andrew Jackson signed into law the Indian Removal Act. In debates leading up to the act’s passage, Congressmen from Georgia argued in favor of removal on the basis that Native peoples were not making good use of the land: God had intended land to be cultivated, and Native peoples had no right to uncultivated lands that white settlers could make more productive (Meyers 2007). Though resistance after the act’s signing resulted in the Second Creek War in 1836, the Muscogee (Creek) were unable to avoid this final expulsion from their homelands to lands west of the Mississippi. The account of a traveler on the Federal Road in July 1836 describe Muscogee (Creek) people being forcibly marched out of their lands, with some choosing to take their own life rather than depart their ancestral homelands for unknown lands in the west (Southerland and Brown 1989).

While the Muscogee (Creek) people were being forced away from these lands, the Black residents of the region were meanwhile forging their own relationships to them. Many retained aspects of the cultural traditions of their African homelands, including the concepts of “good use” of land, wilderness as places of spiritual transformation, and knowledge of natural resources that could be used for food, medicine, and cultural purposes (Johnson 1998, Blum 2002). Their forced labor on Southern farms under the U.S. slavery system also shaped their evolving perspectives on land and place. Enslaved Black residents of the region tended to be more intimately familiar with both cultivated and uncultivated lands than were their white enslavers, as they worked plantation farms and sought refuge and resources from “wild” places (Stewart 2005).

Undeveloped lands—the still-abundant forests and swamps of the region—often served as places of sanctuary for enslaved Black residents. Such places afforded them a measure of freedom from the constant oversight of white society (Blum 2002, Starkey 2005, Stewart 2005, Nielson 2011). In contrast to the large-scale plantation systems found in parts of the Caribbean and South America, in the U.S. South many farms and plantations were relatively smaller-scale, and in most areas Black residents did not outnumber white residents, who sought to be involved in controlling every aspect of Black life (Nielson 2011). Seeking refuge in the “wilderness” provided opportunity for Black people to escape close observation by white people, reinforce kinship bonds by fleeing to visit family on nearby plantations, avoid punishment by their enslavers, hold community and religious gatherings, or plan rebellion (Blum 2002, Starkey 2005, Nielson 2011).

These landscapes also provided enslaved Black communities with material resources. Meager rations supplied to them on plantations could be supplemented by foraged and hunted wild foods, and some obtained cattle or hogs that could be allowed to range on uncultivated wild lands—also providing the opportunity for some personal income with which they could purchase items they and their families needed (Blum 2002, Stewart 2005). Many enslaved Black women developed intimate familiarity with medicinal uses of the native plants that could be found in the wild places surrounding them. They not only applied this knowledge to care for their own communities but were often called upon by their enslavers to treat members of the white household who fell ill or injured (Blum 2002). This knowledge of plant properties additionally facilitated some resistance to the conditions of slavery, as Black women employed plant medicinal remedies to induce miscarriage or—in some instances, with access to their enslavers' food as cooks or household laborers—poison their enslavers (Blum 2002).

Wild places were not viewed only in a positive light by Black residents, however. The threats and unknowns of wilderness were well feared, with many taking care to warn their children of the dangers of panthers and snakes. White women often told similar stories of dangerous wild animals to enslaved Black women and children as a way to control their movements and discourage them from leaving the bounds of plantation life (Blum 2002, Starkey 2005). Persistent concern about venomous snakes led to some Black residents developing a great deal of knowledge and skill in identifying the species they might encounter (Blum 2002). Fears of threats in encounters with other people (both white and Black) or supernatural forces in wild places added to the hesitancy of some Black residents to seek out uncultivated places (Blum 2002).

While enslaved Black residents of the area had somewhat mixed feelings about uncultivated, "wild" places around them, this was in contrast to those of white residents—who more commonly perceived woods and wetlands with hostility, seeing them as places to be feared and dominated (Blum 2002). While wild places held some risks, for enslaved Black persons they also provided important resources and refuge from the cultivated plantations where they were forced to labor. While the roads and paths of the South facilitated the movement of many enslaved Black people into the region, they—and the unseen wild places that bordered them—also served as important venues of escape from enslavement (Jones and Landess 1967, Blum 2002, Starkey 2005, Hudson 2010, Nielson 2011).

Late in the antebellum period, trends in white settlement of—and corresponding transport of enslaved Black persons to—west Georgia lands along the Federal Road had begun to shift. In the 1840s, subscriptions were solicited from Southern residents to fund development of a telegraph line between Macon and Montgomery; as cotton prices had begun to decline, many planters hoped that investment in the telegraph system would provide profitable returns (Cotterill 1917, Wilson 1925). Completion of this section of line in 1848 connected telegraph communication from Washington D.C., all the way to New Orleans, making the Federal Road less necessary for postal communications along that route; however, new railroads being built across the state allowed for easier shipping of agricultural and manufacturing products (Edwards 2001). This included construction of sections of the rail line, operated by the Central Railroad & Banking Company of Georgia (Central of Georgia), that ran along the Federal Route—and adjacent what is now SWMA—through west Georgia just prior to the creation of Taylor County (from portions of Macon, Marion and Talbot Counties) in 1852 and incorporation of the town of Butler in 1854 (Doster 1964, Hellmann 2005).

Despite its position on the new railroad line, the area never became as populated as earlier-established cities such as Columbus to the west, which quickly gained prominence as a major cotton processing, textile and iron manufacturing center of the

South (Edwards 2001). Outside of such urban centers, the South remained even more heavily centered around agrarian life than were many other parts of the country (Stewart 2005). Among statewide tallies of Georgia occupations reported in the 1860 census, farmers and farm laborers represented over 55% of white workers (Kennedy 1864a). Planters were the wealthiest class in Georgia before the Civil War, although this wealth was not evenly distributed—large-scale plantations tended to be the most profitable, and enslaved labor likewise tended to be concentrated on such operations (Wallenstein 1976, Stewart 2005).

In 1860, the Taylor County population consisted of 3,601 white residents and 2,397 Black or mixed-race enslaved residents; no free Black or mixed-race residents or Native residents were documented in the county during that census (Kennedy 1864a). Despite the heavy reliance on agricultural life, less than 30% of the sparsely-populated county had been developed as farmland at that time (Kennedy 1864b).

Post-Civil War

The rural South retained its agricultural leanings following the end of legalized slavery. Environmental and ecological principles were being applied as related to agriculture, with principles of "scientific farming"—such as crop rotation and soil management—gaining popularity (Southerland and Brown 1989, Stewart 2005). Both struggling, small-scale white farmers and newly free Black residents of the area continued to rely on the benefits of uncultivated lands around them, however. Despite centuries of increasing agricultural development, portions of the state still contained substantial amounts of forest cover (Figure 2.2). Residents frequently foraged, hunted, and grazed livestock on these wild "commons" until landowners and landlords began pushing for expanded cultivation and control over access to their lands (Stewart 2005, Ayers 2007). Many of the primary agricultural products of the region became less profitable in the latter decades of the nineteenth century, outcompeted by cheap and large-scale production in newly-settled lands in the U.S. West (Ayers 2007).

In the early years of the Reconstruction era, most Black residents of the country continued to live in the former slave states, where they largely worked in some manner of contract labor for white planters—as wage laborers, sharecroppers, or tenant farmers (Johnson 1998). While in total Black residents acquired ownership of some 15 million acres of farmland across the U.S. South over the decades immediately following the Civil War, this represented a minority of Black residents who became landowners (Johnson 1998, Becher 2023). Those who did purchase land found it difficult to use it in building generational wealth, as inheritance laws disproportionately impacted Black families and resulted in property increasingly divided into smaller fractions or being sold (Becher 2023).

By 1900, these disparities were clear in the “Black Belt”—a term originally used to describe a swath of profitable rich soils stretching across the Southern states, but by that time already applied to instead reference areas with the highest concentrations of Black residents (Webster and Bowman 2008). At the turn of the century, up to two-thirds of white farmers in Taylor County owned the land they worked; in contrast, less than 35% of Black farmers owned the property they cultivated (Ayers 2007). White landlords increasingly flocked to cities for the economic opportunities they provided, giving up most oversight of their lands farmed by tenant farmers or sharecroppers; correspondingly, the late 1800s saw an increase of cash tenancy, as absentee landlords preferred a guaranteed income rather than concern themselves with the productivity of land they were not physically present to supervise (Ayers 2007). The economies of Reconstruction-era farming in the region likely contributed to ongoing shifts in Black perspectives towards land; cultivated lands continued to extract their labor but provide them with little benefit due to extortive landlord practices and unreliable yields (Johnson 1998). At the same time, ongoing racial tensions and the threat of unpredictable mob violence, including execution of Black residents, turned the woods and rural pathways where they had once found refuge into places of increasing danger (Johnson 1998).

Taylor County, still sparsely populated at the start of the 1900s (Harper 1904), underwent further changes in the early decades of the century. The “Great Migration” of Southern Black residents moving to the industrializing cities of Northeast and Midwest—seeking better economic opportunity and escape from the racial tensions of the South—particularly drained the population of rural areas, leaving many communities struggling (Ambinakudige et al. 2012). Still, those Black residents who remained in the South largely resided in such rural communities. Until at least the 1930s, the Black majority of nearly all southwestern Georgia counties resided outside of cities, mostly working on farms (Cable 2013).

Meanwhile, land use in the region began to shift as remaining residents sought more profitable livings and many saw that primary reliance on cotton production was not an indefinitely sustainable economic option for the South. The Central of Georgia began shifting away from efforts to attract new settlers along its railways, as little unclaimed land remained in Georgia. In the early decades of the 1900s the company employed agricultural development agents, industrial agents, and chemists to promote new forms of production among existing Georgia farmers served by its lines (Finlay 1997). These included diversification of agricultural products, growing livestock herds, and new forms of timber and mixed-crop land cultivation. Farmers were encouraged to rotate crops for soil health and to modify land for maximum productivity (Scott 1979, Finlay 1997). Row crops could be planted alongside slash pine (*Pinus elliottii*) for short-term agricultural income; as the pines grew, farmers could benefit from livestock production by promoting pasture grasses in lieu of the region's fire-prone native wiregrass; finally, the pines would provide income from timber harvest or extraction of turpentine (Finlay 1997, Walker 2021). Turpentine production for naval stores was a major part of Georgia's economy through at least the 1930s and, though most often associated with further-south and coastal regions, the industry extended through a swath across this western part of the state (Greer et al. 2015, Walker 2021)—perhaps related to the rail company's promotion of the industry.

During the 1930s the Central of Georgia also pushed farmers along its routes to develop other non-timber forest products and agricultural products for industrial use, such as wood pulp for paper production and sweet potatoes for artificial rubber, cattle feed, and fibers for the textile industry (Finlay 1997). Large-scale sweet potato production failed to take hold in Georgia, hindered by challenges farmers experienced in shifting to cultivation of the larger, starchier varieties and limited facilities for sale and processing of their harvests; by World War II, the Central of Georgia had largely given up pushing this initiative (Finlay 1997).

The postwar decades saw the region increasingly move from agricultural crop production to timber enterprises—particularly in areas with uneven terrain and poor soils for agriculture, such as those found in the Fall Line Sandhills region (Napton et al. 2010; Figure 2.3). Economic changes in the 1970s made it more difficult to profitably export agricultural products, thus driving continued net conversion of farmed to forested lands over the following decades (Napton et al. 2010). Timber production in Taylor County skyrocketed during this period, from 19.5 million board-feet of lumber produced in 1971 to 291.1 million board-feet the very next year (Cathey 1972). In 1985 the federal Conservation Reserve Program was established, which further encouraged farmers to plant trees on degraded farmland soils to combat erosion (Napton et al. 2010)—a problem that had plagued this area since white inhabitation began. Those substantial sands and mineral deposits of the Fall Line Sandhills region also allowed for development of profitable mining operations in the area (Wharton 1989), including the Butler Sand Company that has been in operation to the north of SWMA since the 1950s (Rogers Group 2023).

SWMA area today

Taylor County and other portion of the rural southern Black Belt have largely missed out on the benefits of the "New South," with its rise in technology and manufacturing industries that are a draw for major cities (Ambinakudige et al. 2012). Instead, in many ways its condition has changed little over the past century: it remains highly impoverished, highly segregated, and highly under-resourced. Well over a third of residents live below 200% of the federal poverty rate, and the community lacks necessary infrastructure such as healthcare facilities (Proser et al. 2005). Taylor County is ranked as a county with a persistently high climate vulnerability index (Ryan 2022). It remains a highly racially diverse region, but *de facto* racial segregation persists (Sullivan 2005).

The Taylor County High School garnered widespread media attention for hosting its first (student-organized) integrated prom in 2002—and returning to the practice of separate white and Black proms the following school year (Howard 2004).

Still, ties to the land remain strong for many residents of the area. Large tracts of land bordering and near SWMA were converted from forest and farmlands for the development of the Butler Solar Farm beginning in 2015 (Southern Power 2020)—a common land-use conversion in rural Georgia over recent years (Schnur et al. 2024). Many local residents have serious concern about the construction of large solar facilities in their communities, including the permanent loss of agricultural and forest land, aesthetic impacts, and potential degradation of soils that cannot feasibly be returned to cultivation after conclusion of a power company's lease—sentiments that are reflected by Taylor County residents' expressed perspectives on the sprawling Butler Solar Farm (Schnur et al. 2024, Hoffmann 2024, Interview 1). Land ownership continues to be an important part of rural identities—particularly for white residents—and while they may recognize the need for individuals to gain economic benefit from such leases or sales of their land, many are resistant to land ownership and land-use changes that have the potential to reshape the nature of their communities (Becher 2023, Schnur et al. 2024, Interview 1). These same rural residents often possess more intimate knowledge of their local environments than do more urban residents of similar regions. Studies across parts of west Georgia found that residents of rural, managed pine forest regions tended to score highest on measures of local environmental knowledge, and formal education or income level did not affect local environmental knowledge (McDaniel and Alley 2005). Local environmental knowledge was tied to experience and time spent working in their surrounding forests and fields.

Some echoes of the region's societal history can be directly observed on the landscape of SWMA today. Where travelers once followed the Federal Road, today the Fall Line Freeway (Georgia SR 540) traces the southern border of the east tract (Georgia Department of Transportation 2023). Between it and SWMA runs the railroad line first established by the Central of Georgia over 170 years ago. The limited presence of once-common native plants and the abundance of many nonnative plant and invertebrate species on SWMA reflect historic intensive soil disturbance and fire suppression on the site (Burrow et al. 2021). Such agricultural and silvicultural land use legacies often continue to impact the ecology of restored longleaf pine savannas for many decades after abandonment of those enterprises on a site (Brudvig et al. 2013, 2021, Bizzari et al. 2015). Even conservation and research activities leave traces on the landscape (Figure 2.4).

Implications for conservation

Almost certainly there are local factors I have overlooked or been unable to identify in my attempt to highlight major aspects of intertwined human and ecological histories that have shaped both the landscape of SWMA and the ways in which its surrounding community relates to the land. However, conservation work can benefit from awareness of some of the major dynamics highlighted in those histories—long-term, active shaping of ecosystems by the region's earliest human inhabitants; colonization and efforts to "civilize" the landscape, and the forcible breaking of direct ties between those earlier residents and their homelands; the relationship of centuries of Black residents to both cultivated and undeveloped lands under enslavement; economic challenges and senses of identity that shape ongoing perspectives towards land use and management. These histories not only aid land managers and those involved in species conservation in understanding the current state of the ecosystem, but may provide context for aspects of the social environment around the land's preservation for biodiversity conservation, such as adjacent landowners' concerns about public "ownership" and state government management of the land, reluctance to engage in state agency inquiries to formally expand the boundaries of SWMA, or disinclination to allow state resource managers or outside parties to conduct field surveys for rare species that may occur on their private properties in the area (Interview 1). These histories may inform patterns of which members of the community take advantage of recreational opportunities provided by the land; and they may highlight the conservation resource that could be harnessed by engaging environmentally knowledgeable rural residents who have spent the most time intimately engaging with the landscape through their work and recreation.

Conclusion

A landscape is not separate from its social history. Rather, it is the accumulated manifestation of that history. The ecological forces and social histories I review here are of course particular to a place—if not solely to the small parcel of land and water that today makes up SWMA, largely to its surrounding region. However, I propose that similar attention to the intertwined socioecological context of other lands managed for biodiversity conservation—particularly by agencies, NGOs, or researchers not based within the communities where those lands are situated—would benefit not only the efficacy of conservation efforts but the just practice of engagement with local communities most impacted by that conservation work.

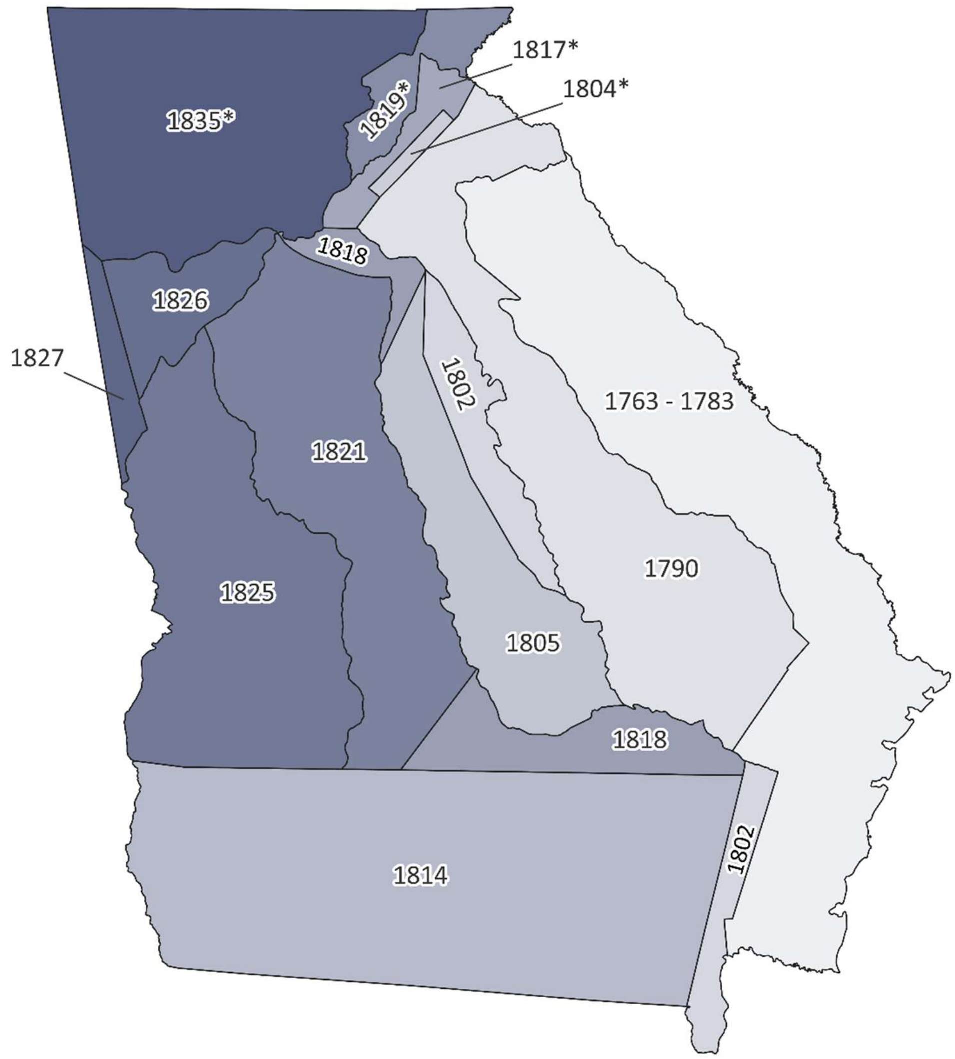

Figure 2.1. Cessions of Native homelands that share geography with the present-day state of Georgia. Northern areas denoted with a (*) indicate Cherokee lands; the rest represent lands of the Muscogee (Creek) confederacy. Dates reflect the year of treaties between members of Native nations and the British-governed Georgia Colony or the federal government of the United States. Created with data from U.S. Census Bureau (2018) and USDA Forest Service (2018).

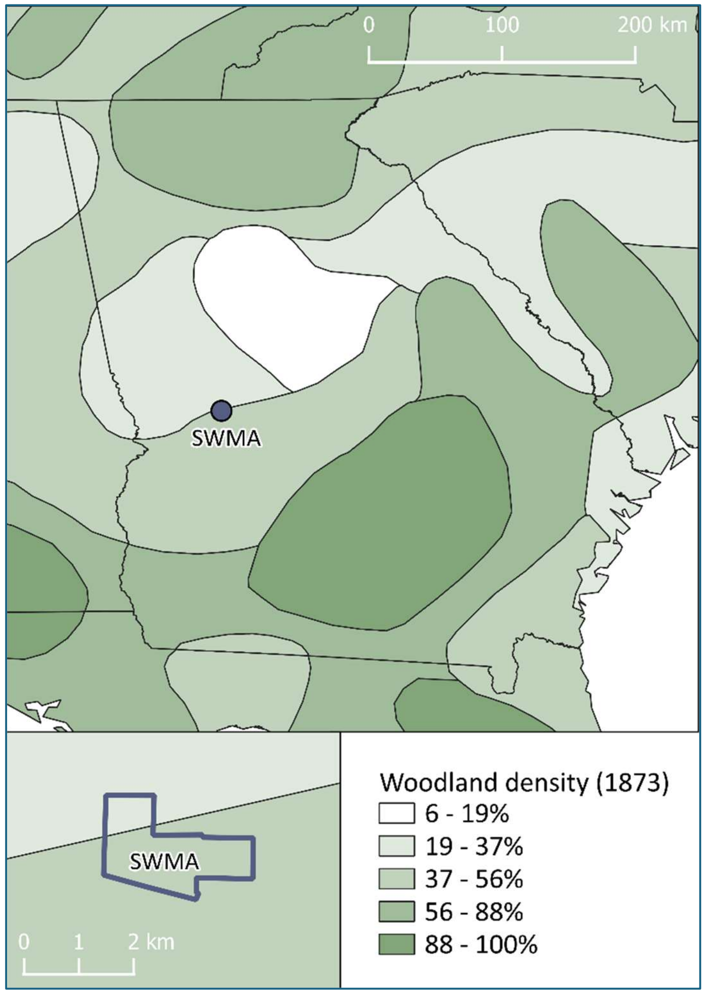

Figure 2.2. Density of woodlands across Georgia in 1873. Present-day location of SWMA shown in inset. Created with data from Liknes et al. (2013) and U.S. Census Bureau (2018).

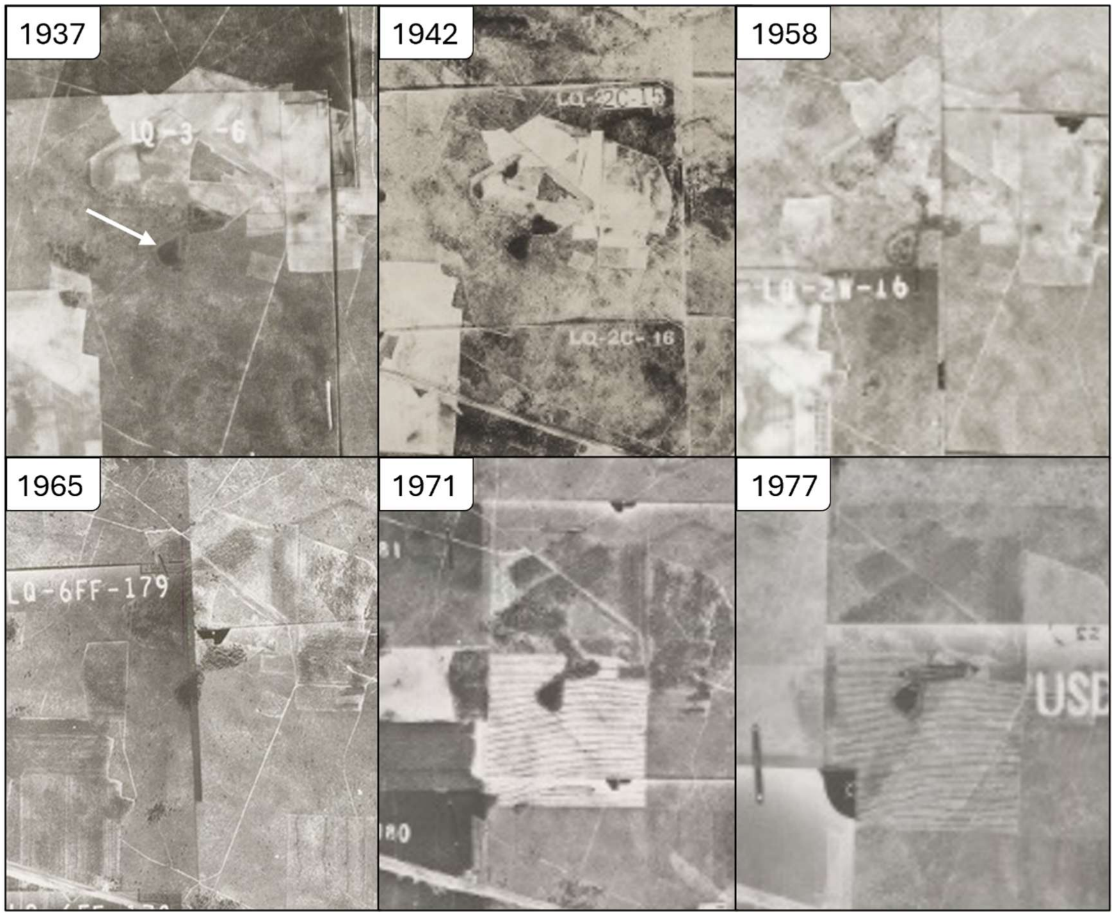

Figure 2.3. Aerial images showing landscape changes northwest of Butler, GA, 1937 – 1977. Each panel shows a similar extent of the area surrounding what is now dubbed Big Pond (indicated by the added arrow in panel A), the wetland on the east tract of Sandhills Wildlife Management Area that supports Striped Newts and other rare or imperiled species. While aerial imagery from this period does not provide the clearest detail, it seems the landscape was heavily influenced by human activity during the middle decades of the twentieth century. At times Big Pond appears quite isolated from any forested or uncultivated upland habitat, such as in 1971 (panel E) when it seems to have a thin buffer of trees or other vegetation, the surrounding tract showing cultivated lines that likely represent planted timber. All images from the U.S. Agricultural Stabilization and Conservation Service, Aerial Photography Division (1937, 1942, 1958, 1965, 1971, 1977), NoC-US.

Figure 2.4. Aerial image showing the effect of conservation research activity near the north end of Big Pond, SWMA (December 2021). The PVC frames of enclosures placed into the wetland for Striped Newt conservation research (see Chapter 4) are visible, as are the lingering paths of researcher movements through wetland vegetation. Image © Google 2019.

Appendix I. Semi-structured interview guide

Interviewee name:

Interviewee title, if applicable:

Interview date:

Interviewer name:

1. How would you describe your role in relation to Sandhills Wildlife Management Area? (E.g., state land manager, area business owner, hunter, other recreational user, area landowner, etc.)
2. Can you provide an overview of how you interact with this property, including any ways that has changed over time?
3. What do you know of the history of this property over time?
4. Do you have any insights into how others in the community have responded to the changing uses of the property over time, including to its current use as a Wildlife Management Area?
5. I'm interested in learning more about the history of how people have interacted with and used this property over time. Is there anyone else you think I should speak to, who may have additional insights to share?

Appendix II. Notes on terminology and group names

Language and history are neither neutral nor subjective (Campbell 2004), and I and readers each bring our own ideologies, perspectives, and cultural contexts to the writing and consideration of the histories described in this paper. Therefore I wish to be transparent about my choices of language used for groups of people and societal circumstances, and to provide clarity about the groups referenced by each term or phrase. The historical accounts and records drawn upon for insight into the human history of this region, particularly relating to marginalized or oppressed groups in society, often contain racial or ethnic descriptors that are explicitly racist or carry derogatory connotations. I do not replicate those terms here; the people-groups being referenced are generally clear from context in the original sources and less-loaded terms can thus be interchanged with little risk of misrepresenting the historical situations described in those accounts.

In discussing peoples who inhabited the region prior to contact with Europeans, I attempt to be specific whenever feasible. Names of Indigenous Peoples were frequently transcribed by white writers attempting to represent the names in their own language (and with varying degrees of care towards faithful representation of phonetic pronunciation), resulting in an array of English-language spellings of the same names (Hemperley 1973). White explorers and residents also often used different group names for Native peoples than those groups used to describe themselves. I here use "Muscogee (Creek)" as that spelling and name format are common descriptors used by the present-era Tribal government within their own official documents and media (Hill 2024). Likewise, I use the name and spelling "Cherokee" in reference to the peoples native to more northern parts of the region, in keeping with the modern Tribal government of Cherokee people in the southeastern U.S. (EBCI 2024). U.S. governmental acts of the pre-removal era generally include only “Creek” in reference to the peoples comprising (or assumed to be affiliated with) the Muscogee (Creek) confederacy; I reference the name of such acts or offices by their official titles.

Where I refer more broadly to “Indigenous” or “Native” residents of the region (such as when used to encompass multiple peoples or when the particular nation referenced in a historical source is unclear), I capitalize the terms in keeping with current usage guidelines put forth by Native-led organizations (Native Governance Center 2024)—while recognizing that “Native” may not be the preferred or most-used self-descriptor of every person or government within those communities today. As the governance and social organization of Native societies during the periods covered in this paper were not always well-understood by white observers, I use the terms “peoples,” “groups,” or “nations” without intent to imply particular structures of affiliation or governance.

Describing African persons trafficked to and enslaved in North America—and their descendants, during and after the era of legal slavery—is similarly complicated by varied and sometimes unclear terms waxing and waning in use over time. Here I typically use “Black” as the most inclusive term to encompass African people trafficked to North America and the descendants of those people (any distinction among places of birth often being absent from the historical sources referenced here), and other individuals of African origin or descent who came to reside in the region, before or after the slavery era. I capitalize the term in keeping with recent advocacy to recognize the term as a proper-noun descriptor for people who share culture, community, and societal experiences, and who because of the legacies of slavery most often are not able to trace their ancestry to specific African nations or peoples. In recent years media groups such as the Associated Press have updated their style guides to include the term “Black” among other long-established, proper-noun terms describing racial or ethnic identities (Daniszewski 2020).

In accounting events prior to the end of legal slavery, I use the descriptors “enslaved” and “free” as relevant to highlight the social and legal circumstances of the individuals or groups referenced. “Enslaved” as descriptor better signifies that being a “slave” is not a natural identity or status of the persons in question, but a condition enforced upon them; many journalists, scholars, and media organizations have begun adopting similar phrasing (Campbell 2004, McBride 2023). Exceptions occur as part of established phrases (e.g., “slave patrols,” “slave states”), where altering wording might hinder clear communication. I use “enslaver” rather than “owner” or “master” in contrast to the idea of humans as property that can be owned by another person.

Except where specifically discussing previous place names, I use the present-day names for cities and landscape features for clarity of context (e.g., “western Georgia” even when the modern boundaries of the U.S. state of Georgia had not yet been established).

CHAPTER 3

POPULATION DYNAMICS OF A STRIPED NEWT (*NOTOPHTHALMUS PERSTRIATUS*) POPULATION IN GEORGIA[4]

[4]Navis, C. J. and J. C. Maerz. To be submitted to *Southeastern Naturalist.*

Abstract

Natural history data on rare species are vital to understanding species ecology and informing conservation decision-making by projecting population responses to threats or management actions. Striped Newts are a highly imperiled salamander species endemic to the southeastern U.S. Just a handful of studies have contributed what is currently known about Striped Newt population dynamics and life history. No studies have detailed dynamics of the few extant Striped Newt populations in Georgia or among the western genetic segment of the species. We conducted capture-mark-recapture sampling over 31 months to estimate the size and structure of what is thought to be among the most robust known Striped Newt populations remaining in Georgia. The population is regularly used as a source for captive breeding and translocation initiatives. Our objectives included documenting the current population status and estimating life stage transition and survival rates for use in a population projection model. Over nearly 200 person-hours of sampling effort, we captured 354 Striped Newts and returned 268 to the wetland with individually identifiable marks. We recaptured only two marked newts, preventing estimation of population size. However, we generated sufficient observations to describe seasonality of detecting life stages and shifts in facultative life stages within the adult breeding population. Our findings indicate a strong tendency to paedomorphic development in this population, as we rarely captured fully metamorphic adults other than immediately following full wetland drying. Detection of sexes and life stages was not constant, with adult females notably absent from samples during summer months. The population dynamics and life history patterns we observed in this Striped Newt population differ from some prior reports, notably in the predominance of

paedomorphosis in this population. Our findings highlight the necessity of understanding geographic or population-level differences among Striped Newt populations when making conservation decisions regarding assessment of population status, habitat management to support Striped Newt populations, or when selecting source populations for translocation and repatriation efforts.

Introduction

Estimates of population sizes and vital rates (e.g., survival, reproduction, and transition between life stages) are essential to prediction of wildlife population trajectories and evaluation of conservation actions (Crouse et al. 1987, Pesarakloo et al. 2020). These basic natural history data are lacking even for many common and well-studied taxa, and the knowledge gap is particularly acute for rare and understudied species (Heppell 1998, Beissinger and Westphal 1998, Katzner et al. 2011). Demographic data are scarce for most amphibians, though they represent the most threatened class of vertebrates globally and there is immediate need for credible models to guide management decisions (Conde et al. 2019, Howard and Maerz 2021).

Striped Newts (*Notophthalmus perstriatus*) are a rare salamander species endemic to the Coastal Plain of the southeastern United States. Striped newts are state-listed as Threatened in both states encompassing their native range, Florida and Georgia (Georgia Department of Natural Resources 2017, Florida Fish and Wildlife Conservation Commission 2022). For decades, researchers and practitioners have been raising the alarm over substantial population declines and extirpations throughout the species' range, and today there are few remaining known breeding populations (Dodd and LaClaire 1995, Franz and Smith 1999, Farmer et al. 2017). Striped Newt conservation is challenged by the species' particularly complex life cycle—even among amphibians—including life stages that are not conducive to *in situ* study and remain quite poorly known (Means et al. 2008, Burton et al. 2012). The few detailed studies of Striped Newt populations (e.g., Dodd and Cade 1998, Johnson 2002, 2003, 2005) focus primarily on drift fence capture of terrestrial life stages seasonally migrating to and from breeding ponds, while little attention has been devoted to characterization of aquatic life stages. Striped Newts are facultatively paedomorphic, and development of larvae directly into mature adult paedomorphs (rather than into a terrestrial, juvenile eft) is likely the default ontogenetic pathway in some populations (Johnson 2005). There have been no studies quantifying the relative prevalence of these developmental pathways within populations (Burton et al. 2012) and the sensitivity of Striped Newts to the environment triggers of alternative developmental routes likely varies among populations due to local adaptation (Wilbur and Collins 1973, Wilbur 1980, Denver 1997, Levis and Pfennig 2019). As a result, there is scarce information to guide management decisions related to Striped Newts. Little is known about how populations respond to habitat changes or management actions, the impact of collection to establish captive breeding colonies, or the efficacy of using translocated or captive-bred newts to supplement or repatriate populations.

The most recently identified extant Striped Newt population in Georgia presents perhaps the best opportunity to study the natural history and demography of a relatively abundant population of Striped Newts in the state. Located within the Sandhills Wildlife Management Area (SWMA), Taylor County, Georgia (Jensen and Klaus 2004), this Striped Newt population is one of few remaining in the state and is among a handful of known extant populations comprising the western distinct population segment (DPS) of the species (May et al. 2011, Farmer et al. 2017). It has been used as a source population for captive breeding and assurance colonies of western Striped Newts (Means et al. 2011, 2013, 2017), although no data exist from which to estimate population size or potential impact of removing individuals from the population.

The objectives of this study were to collect sufficient population data to estimate the size and structure of the SWMA Striped Newt breeding population and key vital rates, including survival rates of various life stages and transition probabilities between larvae, paedomorphic adults, and fully metamorphic adults. These vital rates will be used later to parameterize a Striped Newt population model to guide management decisions.

Methods

Study site

SWMA consists of two disjunct parcels; the ~361 ha east tract was previously a privately-owned timber operation and was purchased by the state in 2007 for conservation of rare plant and animal species that persist on the property (Georgia Department of Natural Resources 2021). Georgia DNR managers are actively working to restore the property to a pine savanna ecosystem and conserve the populations of rare and imperiled species, including Striped Newts. The east tract contains four natural wetlands and three constructed wetlands. The largest wetland, "Big Pond" is ~1.5 ha and currently has a semi-annual hydroperiod, regularly holding water year-round. During this study, Big Pond completely dried in fall 2019 and had greatly reduced water levels in fall 2022, exposing much of the basin and leaving only shallow patches of ponded area. The wetland basin is relatively shallow overall; the greatest depths we observed were slightly over 1 m but more typically reach 0.5 – 0.75 m in the pond interior. The wetland is unshaded, with patchy, abundant maidencane (*Panicum hemitomon*) around the wetland margin. The surrounding uplands consist of the uneven, sandy soils typical of the region, and there remain rows of planted loblolly pine (*Pinus taeda*) from previous timber production on the property, though tree basal area is low from prior thinning and tree death following an intense prescribed fire. Striped Newts have only been detected and documented to breed in Big Pond. Other facultatively paedomorphic salamander species also occur on the east tract. Central Newts (*Notophthalmus viridescens louisianensis*) have been observed in several of the other natural wetlands on the property, but not in Big Pond. Mole Salamanders (*Ambystoma talpoideum*) also breed in Big Pond and paedomorphic adults can be common there. SWMA is open to visitation by the public, including for hunting during permitted seasons, but has no developed facilities and its sandy roads are usually gated against public vehicular access. It was common for us to see no other visitors to the SWMA east tract while conducting research on site.

Sampling methods

Due to the size of Big Pond, it was not feasible to thoroughly sample the entire wetland. Previous exploratory sampling indicated Striped Newts were most easily detected near the perimeter of the wetland where there was dense vegetation and an abundance of submerged logs. Detections of newts or mole salamanders in the center of the wetland were uncommon. Therefore, we concentrated our sampling on a transect around the wetland (within ~5 m of its perimeter).

Each sample consisted of one or more researchers using a dipnet to sample at 5 m intervals around the perimeter of the wetland. All researchers followed the same general track around the perimeter, though they did not necessarily sample at the same points.

Each researcher would pace 5 m from the location of their prior dipnet sweep. We checked dipnets carefully after each sweep, hand picking through vegetation and sediment to check for newts. Our initial plan was to use a “robust” mark-recapture design (Pollock 1982) to account for imperfect detection of individuals. We planned to complete three samples within each primary sampling period (up to two consecutive days); however, logistical constraints presented by the COVID-19 pandemic beginning in March 2020 limited the number of people permitted on sampling trips, extending the time to complete a sample and constraining our ability to extend trips long enough to consistently complete three samples.

Sampling began at the end of August 2019, but Big Pond had dried by October of that year. The wetland filled again in December 2019, and we resumed sampling approximately monthly from January 2020 through December 2021. We additionally sampled in February and March of 2022. In total, we completed 47 samples representing over 195 person-hours of sampling effort.

Captured Striped Newts were placed in individual, labeled reclosable plastic bags with pond water and held in a backpack cooler until they could be transported to shore where they were processed (in warmer months the cooler held cold packs to prevent overheating while we completed each sample). We recorded the location of each capture using either a handheld eTrex 10 GPS device (Garmin International, Inc., Olathe, Kansas) or a satellite image geoPDF in the Avenza Maps mobile app (Avenza Systems, Toronto, Canada).

For all newts, we determined the life stage (larvae, eft, metamorphic adult, or paedomorphic adult; see Chapter 1) and sex, and measured snout-vent length (SVL) to the posterior opening of the cloaca, total length from snout to the tip of the tail (TL), and wet mass. Newts were categorized as adult if their cloaca was visibly swollen; adult males were additionally identifiable by darkened, keratinized toe tips on hind limbs and a visible gland (appearing white to orange under the skin) just posterior to the vent; male cloacae were often more notably enlarged than those of adult females (Johnson 2005). These secondary sexual characteristics were displayed similarly in both metamorphic and paedomorphic adults. Paedomorphic adults have bushy external gills and visible lateral lines, although some display the species' namesake pair of dull to bright red dorsolateral stripes; metamorphic adults do not possess gills and do exhibit the red dorsolateral stripes (Bishop 1941, Johnson 2005). Prior research has established a swollen cloaca and other secondary sexual traits characteristics as definitive characters of individuals with mature reproductive organs (Johnson 2001); therefore, Striped Newts not displaying these mature traits were categorized as juveniles and their sex could not be determined. Larvae possess a similar branchiate form to paedomorphs, while efts resemble metamorphic adults in general body form but have rougher, hydrophobic skin that tends toward an orange-brown dorsal base coloration, in contrast to the tan to dull olive dorsal base coloring typical of metamorphic adults.

Larger larvae (>20 mm SVL), efts, and adults were uniquely marked using visible implanted elastomer (VIE). To minimize stress from time out of the wetland during the hotter months, we did not mark small larvae (approx. ≤20 mm SVL); these were processed and released promptly after capture. After processing, all newts were released at their point of capture. Within typical primary sampling periods, we began subsequent samples ~1 hour after completion of the prior sample when conducted on the same day, or ~17 hours later when samples were completed on consecutive days. On two occasions, we began a sample shortly after (< 20 min) conclusion of the prior sample because we did not capture any newts during the prior sample. On two other occasions, we conducted a sample 6 – 7 days following the previous sample but considered those samples to be within the same approximately monthly primary sampling period.

Results

We captured 354 Striped Newts and marked 268 individuals. In nearly half (42.5%) of samples, we captured fewer than one newt per person-hour of effort. All samples in which we captured > 3 newts per person-hour (4.3% of samples) occurred in January – February or June – August, corresponding with the height of winter breeding activity and peak summer presence of detectable larvae. We only recaptured two individuals, once each. In September 2019 we recaptured a larval newt within the same primary sampling period (the day following initial capture) and near the same capture location; in February 2021 we recaptured a paedomorphic male newt that had been marked 15 days prior, at a point across the wetland from its initial capture location (Figure 3.1). The low number of recaptures precluded us from conducting capture-recapture analysis to estimate transition probabilities of larvae or adults or adult survival rates.

In total we captured 119 adult females and 112 adult males, 8 and 6 of which, respectively, were fully metamorphic while the remainder were paedomorphs. We captured 122 larvae and 1 eft. Life stages detected varied seasonally, with adults most abundant during the winter breeding season and more rarely captured (especially females) from late spring through late summer (Figure 3.2). We generally began capturing larvae by June, when they were ≥12 – 15 mm SVL. Fully metamorphic adults were primarily captured in the winter 2020 breeding season, shortly after the wetland had dried and refilled. By November 2020 nearly all adults detected were paedomorphic, and this remained the case throughout the remainder of the study (Figure 3.3). All classes (sex/morph) of adults had similar mean SVL, but females were heavier than males and paedomorphs were heavier than metamorphic adults. The difference in wet mass between adult forms was most notable among females, although our sample of metamorphic adults across this study was low (Table 3.1). Rather than a clear threshold of size at maturity, there was broad overlap in body sizes of mature and immature individuals. We captured sexually mature adults as small as 27 mm SVL and immature larvae up to 38 mm SVL.

Detections per person-hour of effort substantially differed during the peak breeding activity periods (January – February) in 2020 and 2021, with 0.65 captures/person-hour in 2020 and 2.75 captures/person-hour in 2021. Capture rates during the annual peak periods of larval capture following these breeding seasons (June-August) were similar, with 3.02 captures/person-hour in 2020 and 3.26 captures/person-hour in 2021.

Discussion

Though we captured and marked a reasonably large sample of newts compared to similar studies, we were unable to meet our objectives of estimating transition probabilities of larvae or adults or adult survival rates. However, we were able to generate some important data about population structure and annual cycles of Striped

Newts at Big Pond that can inform a population model and our broader understanding of Striped Newt population dynamics.

Maturity directly into paedomorphic adulthood appears to be the default developmental trajectory among newts in Big Pond at SWMA. Big Pond dried in fall 2019 and had refilled by early 2020 for the typical onset of the Striped Newt breeding season. All adults captured that winter were fully metamorphic forms, as we expected. Because the wetland dried, any larvae or paedomorphs present in late 2019 would have been forced to complete metamorphosis or die. The wetland then remained ponded through the next breeding season, and the probability that an adult Striped Newt captured in winter 2021 was paedomorphic was nearly 100%. In other words, fully metamorphic adult forms were very rare except following wetland drying. Reports on Striped Newts elsewhere in their range have estimated that a minority of larvae develop directly into a paedomorphic form, instead primarily completing metamorphosis and emigrating from wetlands as juvenile efts (Johnson 2005). While we did not have drift fences to detect juvenile eft immigration at Big Pond, the abundance and size of larval newts that we did detect and the rarity with which we detected recently metamorphosed efts or terrestrial adults suggests that metamorphosis into terrestrial juvenile or adult forms is uncommon at Big Pond except when the wetland dries. In a separate study (Chapter 4), we found that Striped Newt larvae from the Big Pond population raised in enclosures within Big Pond overwhelmingly matured into paedomorphic adults, supporting our observations reported in this study.

It is possible that the tendency to complete metamorphosis varies geographically or is density-dependent, as developmental sensitivity to environmental conditions often varies among conspecific populations of facultatively paedomorphic salamanders (Semlitsch and Gibbons 1985, Semlitsch et al. 1990, Newman 1992, Whiteman 1994, Denver 1997). In Eastern Newts (*Notophthalmus viridescens*), both pond hydroperiod (Takahashi and Parris 2008) and upland habitat conditions (Healy 1974) have been identified as factors influencing population-level differences in rates of paedomorphosis. High larval densities have also been shown to induce higher rates of metamorphosis into the juvenile eft stage in Eastern Newts (Harris 1987a, Bohenek and Resetarits 2018). Future studies should aim to determine geographic variation and ecological correlates of life history pathways for this species and determine how density or other environmental factors might affect Striped Newt larval development. This information would be important for guiding decisions about source populations for repatriations or supplementation of populations experiencing environmental change. It would also improve efforts at captive rearing for the rapid recovery or establishment of Striped Newt populations.

We have other anecdotal evidence of limited metamorphosis to terrestrial stages by Striped Newts at Big Pond. Approximately 400 m to the west of Big Pond is a smaller wetland that has been modified to extend its hydroperiod and that contains suitable aquatic and surrounding upland habitat for Striped Newts. As part of Georgia DNR activities and monitoring of other amphibians on the SWMA east tract, that modified wetland has been periodically surveyed prior to, during, and after our study. Several amphibian species including Gopher Frogs (*Rana capito*), which primarily breed in Big Pond, have been detected in the modified wetland, but Striped Newts have not been detected there (N. Klauss, pers. comm.; J. C. Maerz, pers. obs.). Studies of Striped Newts at other sites have documented emigration of efts from wetlands. Johnson (2003) reported primarily efts captured during major periods of emigration from a known Striped Newt breeding wetland, with the majority of breeding adults remaining terrestrially within 100 m of the breeding pond. Similarly, Eastern Newt efts are a primary driver of dispersal to colonize new ponds (Gill 1978, 1979). Eastern Newt efts have been found in high numbers in terrestrial habitat 800 m from the nearest wetland (Healy 1975) and at least one Striped Newt eft has been documented dispersing to a pond 685 m from its natal wetland (Johnson 2003). Based on these observations in other studies, it seems reasonable that if a significant number of efts or terrestrial adults were produced each breeding season in Big Pond, they would likely have dispersed and been detected at the nearby wetland.

While other investigators have suggested that paedomorphic Striped Newts complete metamorphosis as a matter of course following their first breeding season (i.e., at approximately one year of age) (Johnson 2005), our data do not support that pattern in the SWMA population. If no newts remained in paedomorph form beyond their first breeding season, we would expect to see a greater portion of fully metamorphic adults in the breeding population each year. However, we only detected a significant proportion of metamorphic breeding adults in the winter immediately after the wetland had dried. Without wetland drying to trigger metamorphosis, nearly all breeding adults at Big Pond are and appear to remain paedomorphic. Such patterns among facultatively paedomorphic salamanders suggest that the aquatic environment is more favorable than terrestrial conditions, consistent with the “paedomorph advantage” hypothesis of the evolution and maintenance of alternative life history pathways in facultatively paedomorphic salamanders. The paedomorph advantage hypothesis posits that harsh terrestrial environments favor larvae that develop into paedomorphic adults, with paedomorphs experiencing a fitness advantage due to increased growth, survival, or mating success (Whiteman 1994). The plasticity to complete metamorphosis is maintained by episodic unfavorable conditions within the aquatic environment such as wetland drying, proliferation of aquatic predators, or disease outbreaks; additionally, high larval densities may regularly force some smaller larvae to metamorphose and emigrate to surrounding uplands (Whiteman 1994). Under such conditions that select for paedomorphosis as the default developmental pathway, there is no reason to expect newts at SWMA to complete metamorphosis after their first reproductive season unless the wetland dries or aquatic conditions otherwise deteriorate. Notably, rates of paedomorphosis and metamorphosis often vary between populations of a salamander species, indicating population-level selection driven by local environments (Healy 1974, Newman 1992, Whiteman 1994, Denver 1997, Takahashi and Parris 2008). The life history patterns documented in the Striped Newt population at Big Pond thus may differ from those observed in other populations, highlighting the importance of understanding differences in local environmental conditions and population dynamics.

We cannot rule out that the lack of substantial representation of metamorphic life stages at Big Pond is related to extremely low terrestrial survival, but we believe this is unlikely. In the context of population dynamics, eft stages are generally viewed as a slow growing, high survival "storage phase" (DeVore 2011). Eastern Newt efts are known to be highly poisonous throughout a large portion of their range, and that toxicity is linked to high terrestrial survival via predator avoidance. It is said that Striped Newts are similarly poisonous, though we know of no studies quantifying this. Toxicity is known to vary among individual newts and change ontogenetically among efts (Brodie 1968, Ducey and Dulkiewicz 1994), and there is evidence that toxicity varies among populations of *Notophthalmus* spp. as it does among populations of *Taricha* spp. newts in western North America (Hanifin et al. 1999, 2022, Yotsu-Yamashita et al. 2012, Mebs 2019). Assuming efts and terrestrial adult Striped Newts at Big Pond are poisonous, we would expect high terrestrial survival unless the abiotic conditions are too harsh. This is something that would need to be studied. A model of a Striped Newt population in southeastern Georgia predicts that drier conditions will increase upland mortality and limit terrestrial dispersal of newts (Burton et al. 2012). If conditions around Big Pond do not support sufficient terrestrial survival, this means that the Big Pond population is vulnerable to extended drought and isolation from other potential habitat on the property. Management may be needed to improve terrestrial conditions for Striped Newts, as has been proposed for juvenile Gopher Frogs and Ornate Chorus Frogs (*Pseudacris ornata*) on the property (Burrow et al. 2021).

Capture-mark-recapture methods for estimating population sizes and survival rates require that marks are not lost, marks do not increase mortality, and that all animals in the population are equally likely to be captured in a sample or that biases in capture probability among individuals can be estimated and accounted for (Cordero-Rivera and Stoks 2008). We do not believe loss of VIE marks or high post-marking mortality explain our extremely low recapture rate. VIE is a commonly used method for marking amphibians, and numerous studies have demonstrated its retention over time and lack of impact on amphibian survival (Bailey and Nichols 2009, Phillips and Fries 2009, Lunghi and Bruni 2018, Fouilloux et al. 2020, Oropeza–Sánchez et al. 2020). Kopecký (2020) reported loss of VIE marks in Smooth Newts (*Lissotriton vulgaris*) marked during aquatic breeding periods. However, as part of another study (Chapters 4 and 5) we marked adult and larval Striped Newts that were housed in indoor and outdoor conditions (including in enclosures within Big Pond); we observed high retention of VIE tags over numerous months, and no associated mortality. Therefore, the rarity of recapturing marked individuals, even among secondary sampling periods a few hours to a day later, suggests that the capture probability of an individual newt is very low. Further, the seasonal trends we observed in captures indicate that capture probabilities vary among classes of individuals in the population. For example, even though our data suggest that paedomorphic females do not fully metamorphose and emigrate terrestrially after their first breeding season, adult female captures declined markedly after the peak of each breeding season. We do not know where the females go or what microhabitats they occupy, but our ability to capture them is extremely low outside the breeding season. Opportunistic sampling in interior portions of the wetland did not detect adults, and the large wetland area makes discovering Striped Newt use of other wetland areas a daunting undertaking that would require innovative sampling approaches and possibly high researcher sampling effort. In the absence of data on within-wetland movements of aquatic adults throughout annual cycles, care should be taken to compare population measures across similar seasons (and sampled from similar within-wetland microhabitats) so variable detection does not confound interpretations.

While such variability in detection rates—and exceptionally low detection rates overall—can impede reliable estimation of population size (Otis et al. 1978, Schmidt

2003, Ruiz-Gutiérrez and Zipkin 2011), rigorous sampling schemes and analysis that accounts for these detectability factors can facilitate calculation of indices that provide insight into relative population trends (McKelvey and Pearson 2001, Tracey et al. 2005, Kéry et al. 2009). Ongoing study of extant Striped Newt populations is important to characterize population patterns, as high amounts of interannual population variability can contribute to inaccurate conclusions about population trends in response to environmental change or other risk factors or in response to management interventions (McCain et al. 2016). Development of methods to improve detectability of Striped Newts—or to better quantify detectability—would improve the power of statistical methods to detect finer-scale trends in abundance, important to monitoring for population declines or evaluation of positive responses to management actions (Tracey et al. 2005, Bradke et al. 2024).

Additionally, these data from the SWMA population highlight the potential for differences among Striped Newt populations—whether adaptation to local environmental conditions or divergences between the western and eastern subgroups of the species—that may be highly relevant to population assessment and management decision-making. Low tendency to complete metamorphosis other than when forced by wetland drying means that maintenance of longer hydroperiods may be important to population stability. The rarity of terrestrial dispersal in a primarily paedomorphic population leaves an isolated breeding population vulnerable to extirpation, however; populations such as the one at Big Pond may benefit from facilitated introduction to colonize additional nearby wetlands. Population-specific life history and population dynamics are also important to consider when sourcing newts for captive breeding or translocation, as a mismatch between local adaptation of source lineages and conditions of recipient sites may hinder progress towards management objectives.

Table 3.1. Mass and body size of adult Striped Newts captured at Sandhills WMA between August 2020 and February 2022. Body size is represented by snout-vent length (SVL). Values reported are mean ± 1 SE, with number measured in each subgroup reported as *n*.

	Wet mass (g) (*n*)	**SVL (mm) (*n*)**
paedomorphic adult females	2.33 ± 0.04 (*100*)	37.23 ± 0.30 (*111*)
metamorphic adult females	1.84 ± 0.20 (*8*)	36.88 ± 1.27 (*8*)
all adult females	2.30 ± 0.04 (*108*)	37.20 ± 0.29 (*119*)
paedomorphic adult males	1.62 ± 0.03 (*101*)	35.35 ± 0.32 (*105*)
metamorphic adult males	1.48 ± 0.10 (*7*)	36.00 ± 0.87 (*7*)
all adult males	1.61 ± 0.03 (*108*)	35.39 ± 0.30 (*112*)
all paedomorphic adults	1.98 ± 0.03 (*201*)	36.31 ± 0.23 (*216*)
all metamorphic adults	1.67 ± 0.12 (*15*)	36.47 ± 0.77 (*15*)

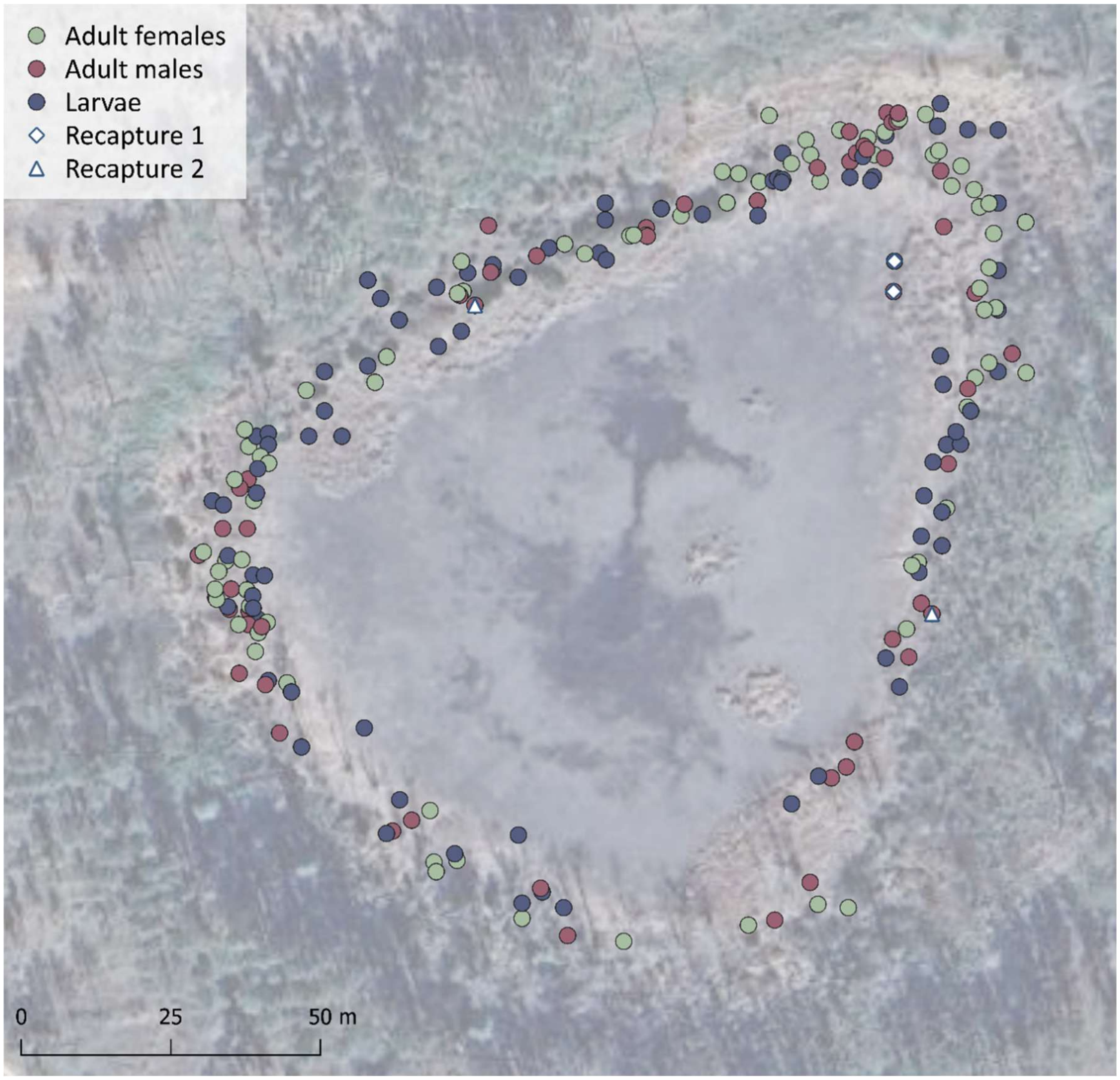

Figure 3.1. Distribution of Striped Newt captures during capture-mark-recapture sampling of Big Pond at Sandhills WMA. While detections were less frequent near the southern end of the wetland, no portions of the wetland perimeter appear to exclude use by Striped Newts. Recapture 1 was a larval newt first captured 31 September 2019 and recaptured the following day, 6 m south of the initial capture location. Recapture 2 was a paedomorphic male first captured near the northwestern edge of Big Pond on 29 January 2021 and recaptured 13 February 2021 near the eastern edge of the wetland (98 m from the initial capture location). Satellite image: Google, ©2024 Airbus.

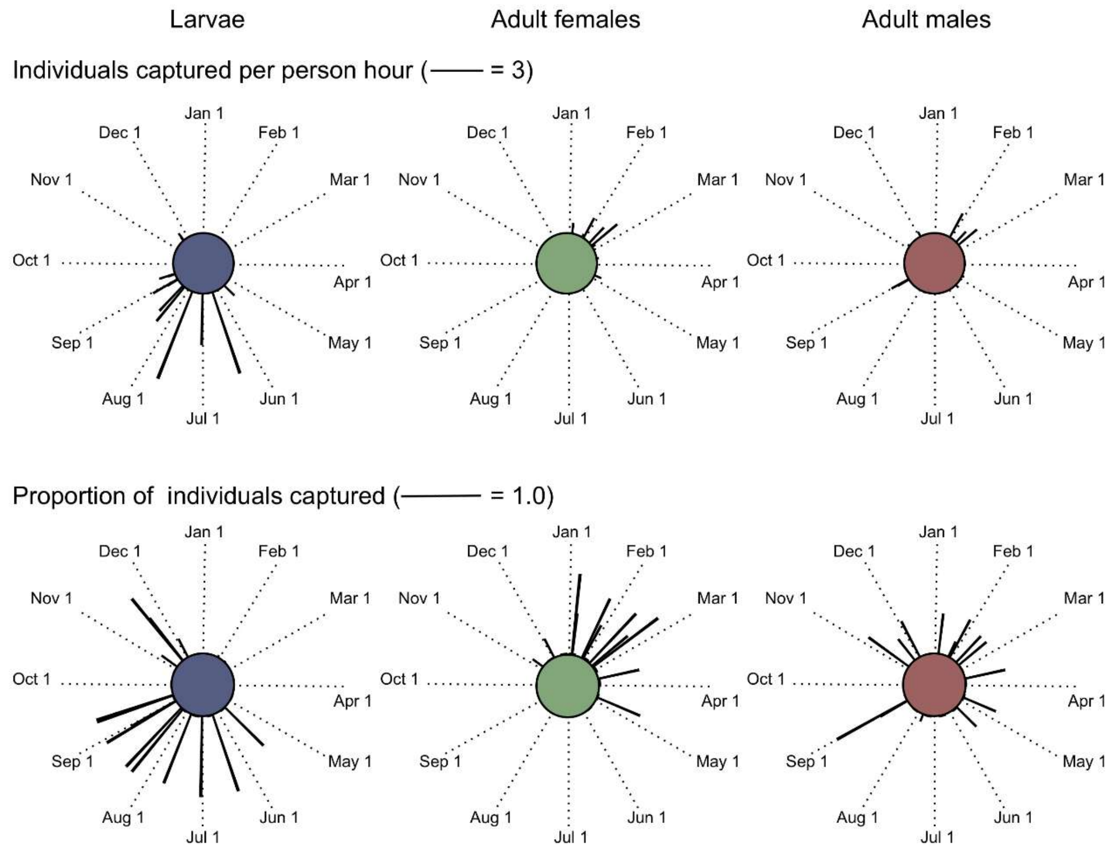

Figure 3.2. Seasonal trends in detection of Striped Newt larvae, adult females and adult males at Sandhills WMA. The same capture data are represented in captures per effort hour (upper panel) and in proportion of all newts captured on a date (lower panel). Larvae (left, blue) were captured in greatest numbers during summer months and were often the only stage detected in those samples. While adult males (right, red) were detected throughout the year, adult females (center, green) were not captured in the summer or early fall of either full sampling year.

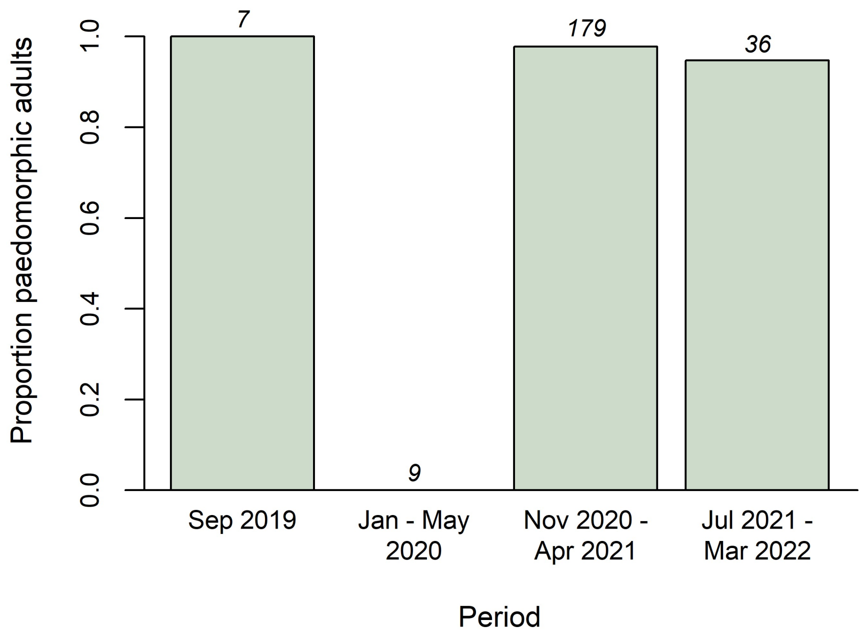

Figure 3.3. Proportion of paedomorphs among adult Striped Newts captured during capture-mark-recapture aquatic sampling at Sandhills WMA. We first captured adults in early September 2019, and the wetland then dried by October; monthly sampling resumed in January 2020. Adults were only captured during the periods shown, generally corresponding with the potential maturation of larvae produced in the prior breeding season and the increasing detectability of adults through the breeding season. The final period includes two paedomorphic males captured in late July 2021; the remainder of adults detected during that period were captured from November 2021 – March 2022. Total number of adults captured during each period is denoted above bars.

CHAPTER 4

EVALUATING STRIPED NEWT (*NOTOPHTHALMUS PERSTRIATUS*) REPATRIATION OUTCOMES TO ILLUMINATE POTENTIAL MISMATCH BETWEEN CAPTIVE REARING PRACTICES AND CONSERVATION OBJECTIVES[5]

[5]Navis, C. J. and J. C. Maerz. To be submitted to *Journal of Herpetology*.

Abstract

Captive breeding has become a popular tool in amphibian conservation. Within the southeastern United States, numerous organizations have collaborated on efforts to boost wild population numbers of an imperiled salamander species, the Striped Newt, via habitat restoration and release of captive-reared larvae. Benchmarks of population growth at repatriation sites have not been achieved on expected timescales, yet it was unclear why released newts have not thrived in those settings as anticipated. Striped Newts have a highly complex life cycle, with multiple developmental pathways likely influenced by environmental factors and population-level differences in sensitivity of response to environmental cues. There have so far been no published studies tracking survival and developmental outcomes of captive-reared Striped Newt larvae after release to evaluate how repatriation efforts might optimize actions to increase Striped Newt population growth and repatriation success. We quantified post-release survival and developmental outcomes among captive-reared Striped Newt larvae reared to different sizes at release into a natural wetland known to support a robust Striped Newt population. Post-release survival was positively correlated with larval size at the time of release, but the probability of developing into a paedomorphic adult declined more steeply with increasing larval size at release. Simulations of the current captive rearing process show that releasing larvae at ~24 mm snout-vent length maximizes the probability that larvae will go on to mature as paedomorphic adults, while holding larvae to near adult size at release is the least optimal strategy for production of paedomorphs despite higher survival after release. Larvae that develop into paedomorphic adults can breed within their first year of life, which is likely critical to rapid population growth. These results

reveal a need to develop captive husbandry practices that will maintain Striped Newts on a paedomorphic developmental pathway. Until then, management targets should be to introduce larvae to repatriation wetlands earlier in their development, meanwhile exploring methods to increase post-release survival. Our study highlights the critical importance of outcome evaluation of conservation and management actions to avoid expending limited resources on counterproductive strategies, particularly for species with complex life cycles and plastic developmental pathways.

Introduction

Recent decades have seen increasing use of amphibian captive breeding for the establishment of survival assurance colonies or to produce young for repatriation to suitable habitat (Tapley et al. 2015, Della Togna et al. 2020). However, less than half of initiatives to reestablish herpetofauna populations are considered to have been successful in achieving conservation objectives (Germano and Bishop 2009, Miller et al. 2014). For most taxa, there exist limited data on how captive breeding may impact suitability of animals for release to their native environments (Mathews et al. 2005). Species with complex life histories require husbandry that considers the needs of multiple life stages and ecological niches, and it can be challenging to avoid detrimental effects to the post-release fitness of captive-reared amphibians (Tapley et al. 2015).

Striped Newts (*Notophthalmus perstriatus*) are state Threatened in Georgia and Florida, which contain the entirety of the species' distribution (Georgia Department of Natural Resources 2017, Florida Fish and Wildlife Conservation Commission 2022). Remnant breeding populations are highly isolated from one another such that natural recolonization and gene flow among wild populations is unlikely (Farmer et al. 2017).

Striped Newts therefore present a need for conservation interventions such as translocation of captive-reared or wild individuals to repatriate restored habitats or to facilitate gene flow between extant populations. Several organizations began establishing captive propagation programs in 2011 to produce Striped Newts for repatriation to suitable habitat (Means et al. 2011). However, these initiatives have not met expected conservation objectives after more than a decade of attempts to reestablish a breeding population of Striped Newts (R. Means, pers. comm.), while expanding captive breeding colonies via regular collection of wild newts from a few extant Striped Newt breeding populations (Means et al. 2017).

Without meticulous monitoring of post-release outcomes, it is difficult to identify the reasons that releases of large numbers of captive-reared Striped Newts have not yet met the objectives of establishing and stabilizing populations. Wild larval amphibian survival rates can be quite low (Wells 2007), so releasing captive-reared larvae too early in their development may result in few surviving to reach maturity. This often leads to the intuitive decision to raise larvae to older, larger stages or through metamorphosis before releasing them as juveniles or adults. However, it is also necessary to consider the potential for carryover effects on an animal's life history and fitness after release (Tapley et al. 2015). Husbandry conditions might result in newts that were held longer in captivity failing to mature as quickly as anticipated or reproduce at expected rates despite improved survival. Indeed, there appear to be developmental impacts of extended rearing in captivity (pers. obs.). Specifically, raising captive-bred Striped Newt larvae to the paedomorphic adult stage, which is believed to promote rapid population growth, has historically proved challenging for captive rearing programs. Instead, captive-bred larvae held longer appear biased to metamorphose into either efts (a terrestrial juvenile stage that can take multiple years to reach maturity) or into a fully metamorphosed and aquatic but sexually immature form (hereafter termed "subadults"). The subadult developmental form has been observed in captive rearing programs but has not been documented in wild Striped Newt populations (Figure 4.1).

While early Striped Newt rearing and repatriation efforts have largely focused on outputs (producing and releasing the maximum number of animals), assessing post-release outcomes for captive-reared newts is critical to evaluating the success of such efforts, identifying needs for adaptation of management approaches, and improving the odds of meeting conservation objectives for the species. Our objective in this research is to assess the survival and developmental outcomes for captive-reared Striped Newts after release into suitable natural habitat. We provide summaries of fecundity and larval survival during captive husbandry, which are useful for modeling and planning captive breeding programs for this species. As paedomorphs are the most abundant breeding adult form in some wild populations, it is important to assess whether and with what probability this life stage versus alternative life stages can be produced through captive-rearing and have the greatest potential to contribute to rapid population growth. We hypothesized that holding and rearing captive-bred larvae longer prior to release would increase survival but reduce the likelihood that those larvae would recruit to the adult breeding population as paedomorphs within the first year of life.

Methods

Source population and release site

Our source population for Striped Newts and location for the release study was a single wetland within Sandhills Wildlife Management Area (SWMA), Taylor Co., GA, USA. The wetland is an approximately 1.5 ha semi-permanent wetland surrounded by pine savanna sandhills habitat. The surrounding property was previously managed as a commercial timber holding until purchase by the state in 2015 (see Chapter 2); it has since been managed for restoration of the historic longleaf pine savanna ecosystem, including regular application of prescribed fire in the uplands and, on one occasion years prior to this study, within the wetland basin. While water levels within the wetland fluctuate annually, the wetland does not typically dry completely each year. Between August 2019 and February 2024, the wetland dried in fall 2019 (no visible standing water) and had substantially reduced water levels and ponded area in fall 2022 and fall 2023. The wetland supports the most recently discovered Striped Newt population in GA (Jensen and Klaus 2004), which is among few known extant populations within the western distinct population segment of the species (May et al. 2011). The SWMA Striped Newt population is also considered the most abundant and apparently stable known population of western Striped Newts remaining in Georgia. Adults can be captured with relative ease during the breeding season, and our own population research documented successful breeding during multiple years of study (Chapter 3). The SWMA population has been a common source for programs establishing captive propagation colonies for the western clade of Striped Newts. We considered both the apparent stability of the population at present as well as its vulnerabilities (reliance on a sole breeding wetland;

unknowns about population size and dynamics making the impact of collections more difficult to estimate) when deciding the minimum number of individuals likely needed to ensure sufficient captive reproduction for this study; collections were undertaken in consultation with Georgia Department of Natural Resources (GDNR) biologists involved in management of the property and species.

Collection of animals

In July 2020 we collected eight larval Striped Newts (20 – 24 mm snout-vent length, SVL) to establish a captive breeding colony in our laboratory facility (Athens, GA). Each newt collected was marked with visible implanted elastomer (VIE) for individual identification so we could track growth, development, and breeding. Within a month in captivity some of the larvae showed reduction in gill size, and by early September 2020 five had fully left the water as terrestrial efts. Only two of these five survived beyond one year of age and their causes of death were unknown. The newts that remained aquatic continued to resorb their external gills and proceeded into the aquatic but immature subadult form, showing no secondary sexual characteristics; prior research has demonstrated that secondary sexual traits are a reliable indicator of internal reproductive maturity in Striped Newts (Johnson 2001). In November 2020 we collected an additional ten larval Striped Newts that were near adult size (30 – 38 mm SVL) from the same source population. By January 2021 these animals all showed secondary sexual characteristics and were considered mature as paedomorphic adults (five male, five female) and were paired accordingly in preparation for breeding. We further supplemented our capacity for the second breeding season of this research by collecting an additional 10 adults (six paedomorphic females, three paedomorphic males, and one fully metamorphic male) from the same source population in November and December 2021. A final, apparently gravid paedomorphic female was collected in late March 2022 and housed alone to deposit eggs prior to return to the source wetland (see Chapter 7).

Husbandry and captive propagation

All larvae, adults, and aquatic subadults were housed in 10-gallon aquaria and fed primarily live blackworms (*Lumbriculus variegatus*), supplemented at times with live *Daphnia*. Adults were housed in pairs, with larvae separated into aquaria by size as growth and size demands required. All aquaria were furnished with multiple artificial aquarium plants for cover and as surfaces for egg deposition. Partial (~50%) water changes of dechlorinated water were conducted on a weekly basis; visible waste and food debris were removed using a baster every second day between water changes. Efts were housed in a 10-gallon terrarium and fed "pinhead" size crickets and flightless fruit flies (*Drosophila hydei* and *D. melanogaster*). Efts were provided continuous access to fresh dechlorinated water and their terrarium was misted regularly. All aquaria were maintained in a temperature-controlled laboratory and were exposed to local daily light cycles via indirect sunlight from nearby windows (blinds prevented direct sunlight on aquaria, to avoid both uncontrolled temperature changes and increased algal growth).

Plants in aquaria with paired adults were checked weekly for eggs. All plants with attached eggs were removed from aquaria on a weekly basis and placed into individual 946 mL deli cups of dechlorinated water until hatching. Counts of eggs were recorded upon collection from aquaria for later calculation of hatch rates.

Upon hatching, larvae were removed from deli cups and transferred to aquaria with larvae of shared parentage and similar hatch dates (up to 25 larvae per aquarium). Beginning within 2 – 3 days of hatching, larvae were provided with brine shrimp (*Artemia* spp.) and *Daphnia*. Within a week or two of growth, young larvae were typically able to eat chopped blackworms. By approximately 20 mm SVL in size, they could eat whole live blackworms. As larvae grew, groups were subdivided into aquaria by size to reduce competition or potential cannibalism. Due to the small size of larvae upon hatching (approx. 8 – 10 mm total length, TL) and housing up to 25 newly hatched larvae per aquarium, it was only possible to confirm counts of live larvae at early stages on these occasions, when we removed all larvae from an aquarium for measurement and to subdivide groups. In 2022, some larvae were produced via captive breeding in outdoor mesocosms (see Chapter 5); data on hatch rates, detailed timing of hatching, and pre-release larval survival could not be obtained for those individuals.

Release enclosures

We constructed six screened release enclosures to facilitate post-release monitoring of captive-reared Striped Newts and placed them within the breeding wetland at SWMA (Figure 4.2). The enclosures were constructed of fiberglass window screening fit around cube-shaped PVC frames of 1.5 m per edge. Each enclosure had a footprint of 2.32 m^2 and internal water volume accessible to larval newts that varied naturally with wetland depth. All seams were tightly hand-sewn using nylon monofilament or braided polyethylene fishing line, and the window screening extended approximately 1.2 m up each side of the frame. Each side was secured by a clip affixed to the top of the PVC frame with paracord to prevent sides of the screen enclosure from drooping into the water. This was a sufficient height to avoid risk of wetland water levels overtopping the enclosures. To prevent tipping, we placed 3.75 L sealed, zip-top plastic storage bags filled with local sand inside each enclosure and anchored the frames with paracord extending to bricks placed on the wetland bottom up to ~3 m from each enclosure.

Upon installation, each enclosure became filled with ambient water from the wetland. We added submerged and emergent vegetation from the area immediately surrounding each enclosure to provide structure and additional inoculation of food sources (e.g., via attached invertebrate eggs). As our goal was to replicate post-release wetland conditions as closely as possible while being able to recapture newts, enclosures were left open at the top to allow colonization by both invertebrate prey and predator species (e.g., dragonfly nymphs, infraorder Anisoptera, or predaceous diving beetles, family Dytiscidae). The enclosure design could not allow passage of larger potential predators or competing species while still retaining the newt larvae, though on one occasion we found a small juvenile (~4.5 cm carapace length) Chicken Turtle, (*Deirocheles reticularia*) within an enclosure (it was released outside of the enclosure as we were uncertain if it could get out on its own). We did not detect any other vertebrates in the enclosures during this study.

Release cohorts

Captive-reared larvae were released into the enclosures in cohorts grouped by size. As Striped Newts have extended egg-laying seasons and we had larvae hatching over a several-month period, these were determined opportunistically based on the sizes and ages of larvae available at a time and aiming for representation across size classes. A total of 241 larvae were released into enclosures in 2021 (Table 4.1), though one cohort of 33 could not be tracked to study completion due to an enclosure tipping over within the month after installation and larval release. In 2022, 36 larvae were released into enclosures, targeting only intermediate larval sizes and ages based on initial findings from the first year of the experiment (one juvenile already in the subadult form was also released in 2022 to monitor its ongoing development). As there are no published data on typical or maximum Striped Newt larval densities in the wild, we determined numbers to release per enclosures based on densities maintained in captivity without apparent competition or cannibalism and on our observation of sometimes high densities of newts within small areas during wild population sampling (Chapter 3). The largest cohort placed into an enclosure was 52 of the smallest and youngest larvae (Table 4.1).

Most larvae released into enclosures in 2021 were not individually marked for re-identification prior to release, though some larvae released later in the season (e.g., when added into enclosures already containing larvae) were given a VIE mark to differentiate between release cohorts or for individual identification. All larvae released into enclosures in 2022 were given uniquely identifiable VIE marks prior to release. We anticipated minimal loss of marks or harm to larvae due to marking, as VIE is widely used in amphibian research and has been demonstrated to be retained well in salamanders and to not negatively impact their survival (Bailey and Nichols 2009, Phillips and Fries 2009, Lunghi and Bruni 2018, Fouilloux et al. 2020, Oropeza–Sánchez et al. 2020). We had observed no mortality and good retention and legibility of VIE marks among the Striped Newts in our captive breeding colony.

Captive larvae were collected from aquaria, measured, and placed into deli containers the day before transport to SWMA. Larger larvae were also marked and weighed at that time (small larvae were typically undetectable on our scales). This allowed us to confirm that the larvae did not experience any immediate impacts from handling and marking, and to assign enclosure cohorts based on the distribution of sizes, ages, and sibships among the larvae planned for release. Across both seasons of larval releases only one individual was found deceased the following day, prior to travel to SWMA. Upon arrival at SWMA, containers of larvae were floated within the release enclosures for a short time to allow water temperatures to equalize and newts to acclimate before release.

Post-release monitoring

Each enclosure was sampled monthly following larval releases; this time interval was selected to limit frequency of disturbance to each cohort while allowing us to collect data on survival and development over time. We used removal sampling (Bailey and Nichols 2009) for estimation of survival rates within each enclosure. Each sampling visit entailed a single researcher using a dipnet to collect newts from an enclosure, in five passes of four minutes each for a total of 20 minutes of removal effort. In each pass, the sampler dipnetted throughout the full area of the enclosure. Each newt captured was placed into a plastic zip-top bag of pond water marked with the pass number. Following completion of all five sampling passes, all recaptured newts were processed and returned to the same enclosure. We recorded VIE marks (if present), presence and estimated length of external gills, length (SVL and TL), any secondary sexual characteristics present, and any signs of injury or other notable observations on individual condition. Newts were not weighed upon recapture due to the challenges of doing so within the wetland. In later sampling occasions following 2021 releases when larvae were sufficient size, recaptured larvae were given VIE marks prior to return to their enclosures to allow continued collection of finer-scale data and estimates of surviving numbers.

If a recaptured newt had clearly matured into a paedomorphic adult, its developmental outcome was recorded and instead of returning it to the enclosure, it was released into the surrounding wetland. This transition was assessed by retention of external gills and presence of secondary sexual characteristics. Secondary sexual characteristics taken to indicate maturity included a clearly swollen cloaca on adult females; this was typically accompanied by a broader and rounded abdomen, though body shape alone was not used to determine maturity and sex. Males were considered mature when we could observe a clearly swollen cloaca (often more pronounced than on mature females), presence of a visible gland cluster posterior to the vent, and keratinized toe tips on the rear limbs (male Striped Newts do not develop visible femoral pores as are obvious on male Eastern Newts, *N. viridescens*) (Dodd 1993). Prior Striped Newt captive propagation research has verified that these secondary sexual characteristics reliably correlate with internal reproductive organs (sex) and stage of internal reproductive development (maturity) (Johnson 2001). Any recaptured newts that had matured into a metamorphic adult (i.e., loss of external gills but presence of secondary sexual characteristics) were also released into the broader wetland following final data collection. Recaptured newts that were still in the larval stage or had transitioned into the subadult stage were returned to the enclosure after data collection.

Each season of monitoring concluded when we could not detect any newts remaining in the enclosures or when wetland drying necessitated emptying of the enclosures to release remaining newts. At annual completion of monitoring, we lifted each enclosure from the wetland and manually removed vegetation and sediments to determine if there were any undetected newts. Most enclosures stocked with larvae in 2021 were sampled through February 2022, by which time all larvae had died or transitioned to another life stage. A single enclosure stocked in 2021 held newts until May 2022. Enclosures stocked with larvae in 2022 were emptied of all remaining newts in mid-October due to persistently diminishing water levels within the wetland.

Data analysis

Because we did not directly observe most instances of mortality among captive larvae, we used numbers of surviving larvae confirmed periodically (i.e., when removing all larvae from an aquarium) to track larval mortality during captive rearing. Due to transfer of larval cohorts to field enclosures at varying ages, we could not directly calculate the percentage surviving in captivity by age after hatching. Instead, we estimated a non-parametric survival function using the survfit tool in the R "survival" package, which uses Turnbull's maximum likelihood estimator to accommodate data with censored observations due to removal of individuals from ongoing monitoring (i.e., larvae released to experimental enclosures) and when mortality is known to have occurred in a discrete time interval but the exact date is unknown (Turnbull 1976, Dehghan and Duchesne 2011, Rodrigues et al. 2018). All larval ages were calculated from the mean of hatch dates represented among co-housed larvae (mean range of 11.81 ± 0.34 SE days).

We used logistic regression to test the hypotheses that larval SVL at time of release was positively correlated with post-release survival beyond the larval stage and negatively correlated with the probability of developing into a paedomorphic adult. We then used a Monte Carlo simulation to estimate the median number of paedomorphic adults produced per 1,000 released larvae. For each larval release size (3 – 33 mm SVL), the simulation drew the probability of post-release survival to the end of the larval stage and the probability of subsequently developing into a paedomorph from the corresponding logistic regression models to jointly estimate the number of those 1,000 released larvae that would survive and eventually develop as paedomorphic adults. The simulation was repeated over 100,000 iterations for each target larval size at release to estimate the median number of adult paedomorphs per 1,000 larvae released.

Results

Captive propagation

Breeding females began depositing eggs onto artificial plants in their aquaria beginning in early February 2021. Three females accounted for all eggs laid in 2021; one of these females deposited only 3 eggs, only one of which hatched but the larva was deformed and did not survive long. One female laid 157 eggs (93.1% hatch rate). Another female initially laid 124 eggs (90.3% hatch rate). Following pairing with a different male (and approximately 19 days after her most recent egg deposition) she apparently began a second “clutch” totaling 203 eggs (75.9% hatch rate). In total, we observed an 84.8% hatch rate among all eggs laid in 2021.

In 2022, newts breeding in indoor aquaria began oviposition in late January but produced fewer eggs and at slower rates than during our first captive-breeding year. This included reduced output from one female (the most productive female in 2021 laid only 24 eggs over the span of 73 days the following year), but with three females producing eggs for the first time in 2022. In total, four captive-mated females in our laboratory facility deposited 70 eggs in 2022, with a far lower hatch rate than the prior year (40% overall); an additional 21 juveniles were collected from outdoor mesocosms, 12 of which were still in larval form and were included in this study (others had transitioned into metamorphic, immature life stages prior to retrieval; see Chapter 5 for more details). The female collected from SWMA in March 2022 deposited 11 eggs, though primarily on the floor of her aquaria rather than attached to artificial plants; they were carefully transferred to deli cups, but none hatched or clearly developed.

Among larvae hatched and reared indoors there was substantial mortality (41.21%) before larvae had reached target sizes for release to field enclosures. (Potential mortality among larvae in outdoor mesocosms is discussed in Chapter 5.) Nearly half of that documented attrition was in larvae under 40 days old. Median survival time in captivity was estimated to be 70 days after hatching (Figure 4.3), although confidence of estimates of captive survival is greatly reduced with increasing larval age due to few individuals retained in captivity to late in larval development (Prinja et al. 2010, Barrajón and Barrajón 2020). We observed no evident causes of larval mortality, generally detecting attrition only during periodic censusing of each aquarium.

The subadult newts observed longest in our facility included three of those collected as wild larvae in July 2020 and two that were produced via captive breeding in 2021 and were not released to wetland enclosures. Those two captive-reared larvae had transformed into subadults within five and seven months after hatching, respectively. There was wide variation in the time captive subadults remained in that immature form before displaying secondary sexual traits indicative of maturity, ranging from one to 27 months (mean 12 ± 3.93 months) among these five newts. All five matured as males.

Seven larvae produced in the 2022 captive breeding season transitioned into the subadult stage prior to release and had not yet matured by November 2022 when we concluded captive husbandry.

Post-release outcomes

Five removal passes per enclosure were not sufficient to deplete populations to a point of diminishing captures per pass (Figure 4.4), making it impossible to generate precise estimates of capture probability or unbiased estimates of monthly Striped Newt abundance and survival in each enclosure. Therefore, we relied on data of larvae we recaptured after they had survived to transition into another life stage to estimate survival and development rates. Thus, we cannot provide any information on temporal patterns of mortality within enclosures but only final outcomes.

We did not recapture any individuals from the two cohorts of smallest larvae. We recaptured newts from all other cohorts, and all cohorts included at least one individual observed to have survived beyond the larval life stage (Table 4.1). Across both release years, 35 of 245 larvae were recaptured after transitioning out of the larval stage. Of those 35 newts, 24 had matured as paedomorphic adults (12 female, 12 male). Seven had transitioned into the immature subadult stage, and four had become metamorphic adults (all male). Subadults were smaller when first recaptured in that life stage (26.14 ± 1.35 mm SVL) than were metamorphic adults (32.75 ± 0.63 mm SVL) or paedomorphic adults (33.38 ± 0.86 mm SVL). Males matured as paedomorphs at smaller body sizes (31.58 ± 0.74 mm SVL) than did females who became paedomorphs (35.16 ± 0.74 mm SVL). Both survival and the probability of developing directly into a mature paedomorph were significantly correlated with larval size at release (Figure 4.5). Probability of survival beyond the larval stage increased with SVL at time of release (estimate = 0.121, SE = 0.024, z = 5.151, $p < 0.001$), while the probability of maturing directly following the larval stage declined with SVL at release (estimate = -0.900, SE = 0.340, z = -2.615, p = 0.009).

Simulations showed that releasing captive-bred larvae at ~24 mm SVL is predicted to maximize the number that would become reproductively mature paedomorphs after release (Figure 4.6). Holding larvae in captivity to larger sizes results in a rapid decline in the number of paedomorphs expected to result from the same number of released larvae, as continued increases in post-release survival do not compensate for the developmental impacts observed in captive-reared larvae released late in development. In fact, retaining larvae in captivity beyond 28 mm SVL is projected to produce fewer paedomorphs than would result from releasing larvae immediately after hatching, despite substantial differences in post-release survival (Figure 4.6).

Discussion

It is apparent from the outcomes of our released newts that common captive propagation methods for Striped Newts and decisions about the timing of release are likely impacting the post-release survival and development of those animals. Our results indicate that despite increasing survival to subsequent life stages, delaying release of captive-bred larval Striped Newts substantially reduces the likelihood that they will develop into a paedomorphic adult and be able to breed within their first year. Instead, holding larvae to larger, near-adult size before release increases the likelihood a Striped Newt will metamorphose into an immature subadult with an undetermined delay in breeding. Thus, the aim of increasing larval survival by holding larvae longer for rearing to a larger body size has diminishing returns, as extended duration of larval development in captivity is counterproductive to the objective of producing paedomorphic adults who will mature quickly and contribute to rapid population growth.

Our captive propagation data also provide important insight into larval mortality during captive rearing. We are not aware of any published reports documenting survival and attrition rates of captive-bred Striped Newt larvae while in captivity. Without regularly censusing captive-reared larvae, it can be incredibly easy to believe that little to no attrition is occurring. Only rarely did we observe any deceased larvae; carcasses of salamanders, and especially those of aquatic salamander larvae, can disintegrate rapidly in water (Brand et al. 2003, Regester and Whiles 2006). Even during periodic larval counts, rates of mortality among small larvae were not immediately apparent. While the survival estimates shown in Figure 4.3 are aligned to larval age since hatching, those data represent hundreds of total larvae hatched across nine months of two breeding seasons; losses were most commonly detected as a relatively small reduction in the number of larvae present in an aquarium since the last full count. Identifying larval mortality in captivity means that decisions about timing of releases must weigh the relative survival risks of both the pre-release and post-release environments. Pre-release mortality not only reduces the number of animals available for release but may reflect other effects of captive husbandry on the phenotypes of Striped Newts produced through captive breeding. Mortality among environmentally sensitive larvae early in development may indicate selection for conditions of the captive rearing environment, potentially reducing overall cohort adaptation to their natural habitat (Michaels et al. 2014, Tapley et al. 2015). This concern is amplified with increasing generations of captive rearing, such as retaining F1 larvae for breeding or attempting to establish a long-term survival assurance colony (Frankham 2008). Documenting and identifying drivers of pre-release larval mortality may be an important element of adapting husbandry approaches to avoid altering the fitness of captive-reared newts in natural environments.

It is not possible for us to know exactly how post-release threats to larval survival inside our enclosures compared to those larvae would face in a "hard release" directly into a wetland. Our enclosures necessarily reduced risk from some potential predators but limited newts' access to varied wetland microclimates that can be vital for amphibians (Michaels et al. 2014). However, we expect that similar rates of larval survival are likely in wild Striped Newt populations, with low overall survival from hatching through maturity. The regression model of our survival data (Figure 4.5) predicts a baseline of 2.8% survival from approximate hatchling size (3 mm SVL), which is a reasonable rate of larval survival in aquatic amphibians. Single-digit percent survival of larvae to subsequent life stages is not uncommon for amphibians (Wells 2007). In the absence of data on wild larval survival or post-release survival of translocated Striped Newts, we consider our results to represent a reasonable estimate of expected patterns of survival after release.

No age- or size-specific survival data are available for free-living Striped Newts, and we cannot estimate from our data if mortality risk varies over the course of the larval stage. However, survival to a mature adult stage is a highly relevant metric when considering the likelihood that a translocation effort will reach key benchmarks of success. It is important for released animals to not only survive in the short term but to reach maturity and breed. It is unsurprising that releasing newts later in their larval period improves their odds of surviving to the end of that stage; however, if that survival does not result in reproductively mature individuals, such benchmarks of repatriation success will be delayed or may not be achieved at all. While our estimations of larval survival are not atypical among amphibians, such high larval mortality is generally compensated for by high egg production. Clutch sizes among pond-breeding amphibians can range from hundreds to many thousands (Mitchell and Pague 2014). It appears that Striped Newt annual fecundity is on the lower end for aquatic-breeding amphibians, which means that rapid population growth likely depends on large numbers of breeding females and rapid maturity to first reproduction.

Population persistence with relatively low fecundity and high larval mortality may also depend on high adult survival. There exist few data with which to estimate longevity of free-living adult Striped Newts. Low aquatic detectability can be an obstacle to capture-mark-recapture investigation of Striped Newt life history (see Chapter 3) and reports of population studies do not always present data on recapture rates that might facilitate such estimations. While there are reports of adults surviving to at least 12 years of age in captivity (Means et al. 2008), wild adult survival is likely lower. In some populations of Eastern Newts, adult female life expectancy was estimated to be less than two breeding seasons (Gill 1978). Dodd (1993) reported data on marked Striped Newts recaptured at terrestrial drift fences during an extended drought that suggest that—at least under some environmental conditions—there may be similarly high annual turnover of breeding adult populations in Striped Newts. Nearly 17% of marked newts were recaptured within a year after first capture, but recaptures declined sharply to <1% in the second and third years after marking and no marked newts were recaptured after four years (Dodd 1993). Those data suggest that terrestrial survival of metamorphic adult and juvenile Striped Newts may be low, and thus reliance on the survival of metamorphic juveniles (subadults or efts) to maturity may not be sufficient to produce desired population growth.

It is reasonable to assume that the subadult newts commonly produced with current captive breeding approaches will breed eventually, thus contributing to reproduction with perhaps only a brief lag in population growth. At present, we caution against this assumption. We did observe eventual maturation from the subadult stage in some individuals in our captive husbandry facility and within release enclosures; however, we observed only males maturing into metamorphic adults from the subadult stage during our study and time to maturation was quite varied among those males. Maturation of subadult females appears likely to be delayed even longer. Adult female Striped Newts are typically larger (particularly by mass) than males (Dodd 1993, Johnson 2002; Chapter 3); this pattern is common in salamanders and results from a positive relationship between female size and fecundity (Salthe 1969, Malmgren and Thollesson 1999, Marzona et al. 2004). Females that metamorphose into small subadults may require substantial growth to reach reproductive size, but growth following metamorphosis is often gradual in newts. *Notophthalmus* efts typically exhibit slow growth over extended periods (up to several years) until maturity (Healy 1974). Thus, we believe that the evidence to date indicates that release of older, larger larvae or metamorphic subadults is unlikely to result in most individuals—and particularly females—recruiting into the adult breeding population for several years. When few captive-reared animals recruit to the breeding population in the near term, there may be little benefit to population growth or persistence (see Chapter 6). Our study of natural breeding dynamics in the SWMA Striped Newt population (Chapter 3) showed that most breeding adults are paedomorphic individuals that can breed within the first year, unless a wetland dries and triggers completion of metamorphosis. This suggests that rapid maturation is likely the adaptive life history pathway and carries higher fitness for Striped Newts. It is possible that for populations occupying sites with shorter hydroperiods and where wetlands dry regularly, the production of paedomorphic adults may offer less benefit towards rapid population growth.

Future directions

Based on the demonstrated impact of captive husbandry on the development of Striped Newts, we suggest three complementary paths forward to improve outcomes of captive rearing and translocation efforts for the species: 1) using these findings to guide the timing of larval releases to maximize benefits to population growth; 2) conducting research to identify triggers of these developmental effects and adapting captive husbandry procedures accordingly; and 3) researching methods to improve post-release survival of small Striped Newt larvae.

Our results indicate that there is a critical period in larval Striped Newt development that strongly influences whether an individual may mature directly into a paedomorph or will develop into another, metamorphic life history stage. The apparent developmental impacts of captive conditions, once triggered, appear to persist after release, as many larger larvae that retained external gills at time of release nonetheless proceeded to metamorphose into the immature subadult form. Our simulations predicted the greatest number of paedomorphic adults produced by targeting release of larvae at 24 mm SVL. Because the probability of paedomorphic development drops off steeply beyond that release size, it may be advisable to err on the side of earlier release to avoid non-target developmental pathways.

Investigation into the conditions that most influence Striped Newt larval development could inform adjustments to captive husbandry protocols and mitigation of the carryover effects documented in this study. Abiotic factors and the effects of larval rearing density are two potential areas for further research. Numerous abiotic conditions differ between natural Striped Newt breeding wetlands and typical captive rearing environments, and some of these differences may be relevant to the documented developmental effects. For instance, dissolved oxygen concentrations have been shown to impact gill retention and rates of metamorphosis in other aquatic salamanders (Carter 1997, Segev et al. 2019). Common Striped Newt larval rearing densities may be adequate to avoid cannibalism or food competition, but research on the life history effects of larval density in Eastern Newts has indicated that high larval density—independent of food limitation—can trigger higher rates of metamorphosis rather than development into paedomorphic adults (Bohenek and Resetarits 2018). If captive husbandry protocols can be adapted to reduce developmental consequences for captive-reared Striped Newts, survival could be improved by releasing larvae at larger sizes while still allowing natural development into mature paedomorphic adults.

Another approach is to release larvae early in development but experiment with methods to improve post-release survival. One consideration is the use of “soft release” enclosures, which would both facilitate post-release monitoring to determine near-term repatriation outcomes and reduce threats to small and intermediate sized larvae.

Enclosure designs could be modified to reduce mortality in the field (e.g., fully enclosing them to limit invasion by invertebrate predators), thereby increasing the survival of small larvae that are more likely to mature into paedomorphic adults. Similarly, developmental consequences of captivity might be avoided by translocation of reproductive adults—whether for direct release into recipient wetlands or to deposit eggs in similar protective enclosures—allowing larvae to develop entirely in the conditions of the recipient wetland. Such translocations of adult females to lay eggs within soft-release enclosures at recipient would also circumvent the potential for selection of traits favored by the captive rearing environment but less well-suited to the natural environment (Tapley et al. 2015).

Conclusion

Understanding outcomes for animals released from captive breeding programs is vital to making efficient use of limited conservation resources and achieving species management goals. The tradeoffs we documented between survival and developmental trajectories illustrate that not all captive-reared Striped Newts will experience the same post-release outcomes. Conservation planners should thus carefully consider which release sizes and life stages are most likely to achieve progress towards their conservation objectives. Rearing larvae to larger sizes or to maturity involves higher husbandry costs, which may be a constraint on captive rearing programs (Rogers and Banulis 2003, Canessa et al. 2014). If population-scale benefits decline with extended time in captivity, institutions involved in captive propagation efforts can both reduce resource demand and make better progress towards repatriation objectives by ensuring larvae are released before they are developmentally limited by extended time in captivity, even if post-release survival rates may be somewhat lower (see also Chapter 6).

Our findings further illustrate the cruciality of post-release monitoring and ongoing evaluation of repatriation efforts, as outputs (i.e., numbers of animals produced or released) do not always translate into anticipated species conservation outcomes (e.g., population growth). Additional research may reveal that the specific release sizes indicated by our results may not be ideal for all situations, e.g., if there exists population-level adaptive variation in the propensity to facultative paedomorphosis, particularly among source populations. However, this study highlights the importance of empirical evidence to inform husbandry and management practices (Tapley et al. 2024). The results of repatriation actions cannot be intuited or assumed; evaluation of outcomes and ongoing adaptive management are critical to improve chances of achieving benchmarks of success and effectively conserving Striped Newts in the wild.

Table 4.1 Characteristics and outcomes of release cohorts of captive-reared Striped Newt larvae. Mean snout-vent length (SVL) and mean age are at time of release into wetland enclosures.

Release cohort	Release date	Cohort size (*n*)	Mean SVL (mm)	Mean age (estimated days since hatching)	Confirmed survived past larval stage (*n*)	Matured as paedomorphs (*n*)
A	30 May 2021	41	6.12	43	0	-
B	30 May 2021	52	6.41	38	0	-
C	25 June 2021	14	15.05	98	1	1
D	25 June 2021	12	15.21	92	1	1
E	16 Aug 2021	50	11.29	51	9	9
F	16 Aug 2021	33	16.30	64	*no data due to enclosure malfunction*	
G	11 Sept 2021	13†	25.15	107	2	2
H	11 Sept 2021	13‡	24.85	107	8	6
I	20 Oct 2021	7†	26.86	219	2	1
J	20 Oct 2021	6‡	28.33	227	5	0
K	2 July 2022	12	27.33	107*	1	1
L	2 July 2022	12	27.25	106*	2	2
M	11 Aug 2022	8	22.88	93	1	1
N	20 Aug 2022	4§	32.00	NA*	3	0

* Age not estimated for larval cohort *N* as they were hatched in outdoor mesocosms. Seven of the larvae released 2 July 2022 (four in cohort *K* and three in cohort *L*) were likewise hatched in outdoor mesocosms; the age estimates listed for those two cohorts is a mean of the larvae hatched indoors.

† Larvae in cohort *I* were added to the same enclosure as cohort *G*; individuals in cohort *I* received a cohort VIE mark to distinguish the cohorts within the same release enclosure.

‡ Likewise, cohort J was given a cohort VIE mark and released into the same enclosure as cohort H.

§ The listed number in cohort N represents the individuals released still as larvae; an additional mesocosm-hatched juvenile that had already proceeded into the subadult stage was also released as part of that cohort to monitor survival and potential maturation.

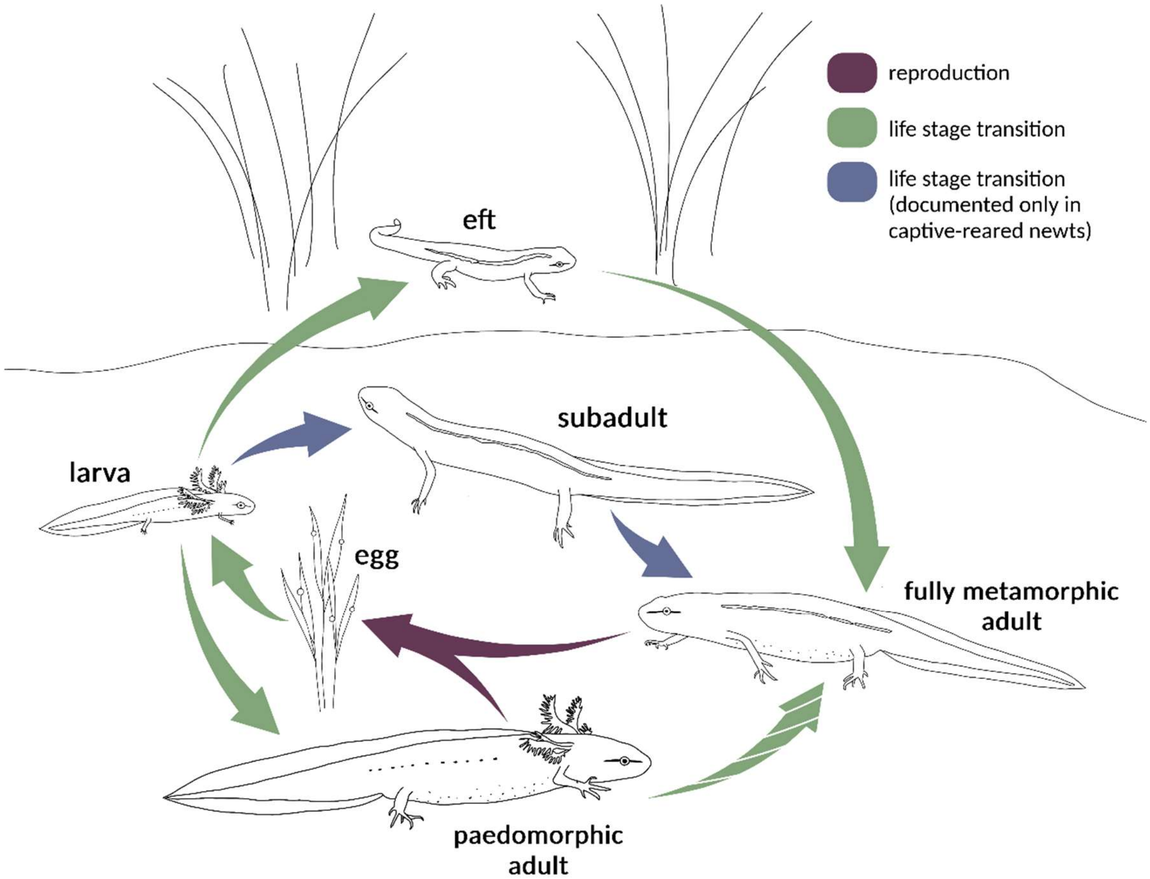

Figure 4.1. Life cycle of Striped Newts in wild-breeding and captive-reared populations. The subadult developmental pathway is only known to occur in captive-reared larvae (or wild-collected larvae that likewise spent early development in captivity). Transition from paedomorphic to fully metamorphic adult is shown with a dashed arrow as when wetland conditions allow, in at least some populations this transition is not automatic.

Figure 4.2. Release enclosure used to allow for post-release monitoring of larval Striped Newt survival and development.

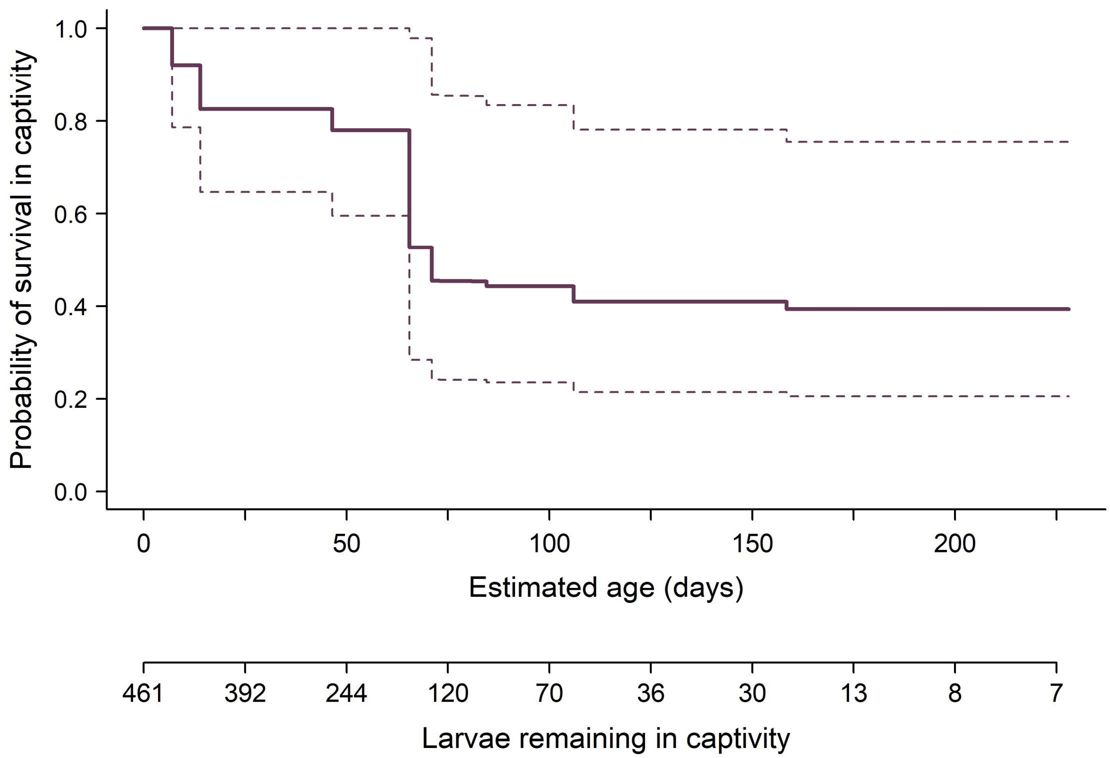

Figure 4.3. Survival curve for captive-reared Striped Newt larvae prior to release into wetland enclosures. The solid line represents the survival function, which can be interpreted as the estimated probability of survival to each age had all larvae remained in the captive population (i.e., not removed by transfer to release enclosures). Abrupt "steps" in the survival curve appear because mortality could only be confirmed periodically, and the remaining captive larval population declined steeply with age as cohorts were released to field enclosures. Remaining *n* under observation in the captive population is denoted on the lower x-axis and aligns to larval ages shown on the primary x-axis. Dashed lines represent 95% confidence intervals.

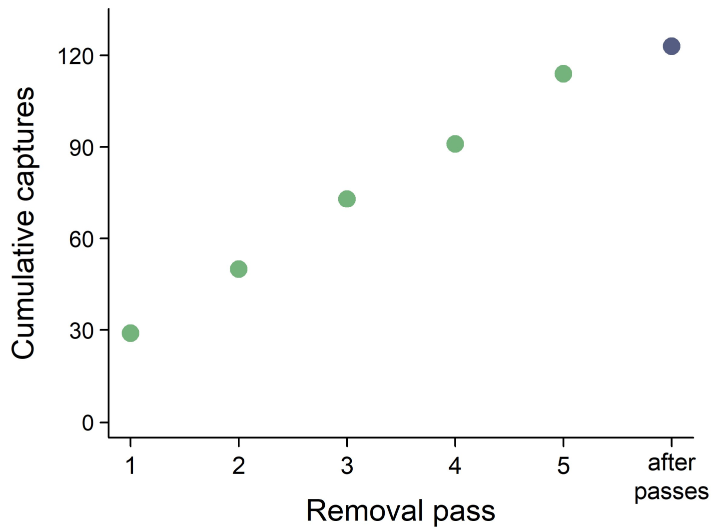

Figure 4.4. Cumulative captures by removal sampling pass in Striped Newt wetland release enclosures. Points represent the sum of captures per sequential removal pass across both years of enclosure sampling. The final "after passes" value (blue point) includes newts detected following completion of the standard removal sampling passes, i.e., via additional dipnetting or manual searching of enclosures at the end of a monitoring season.

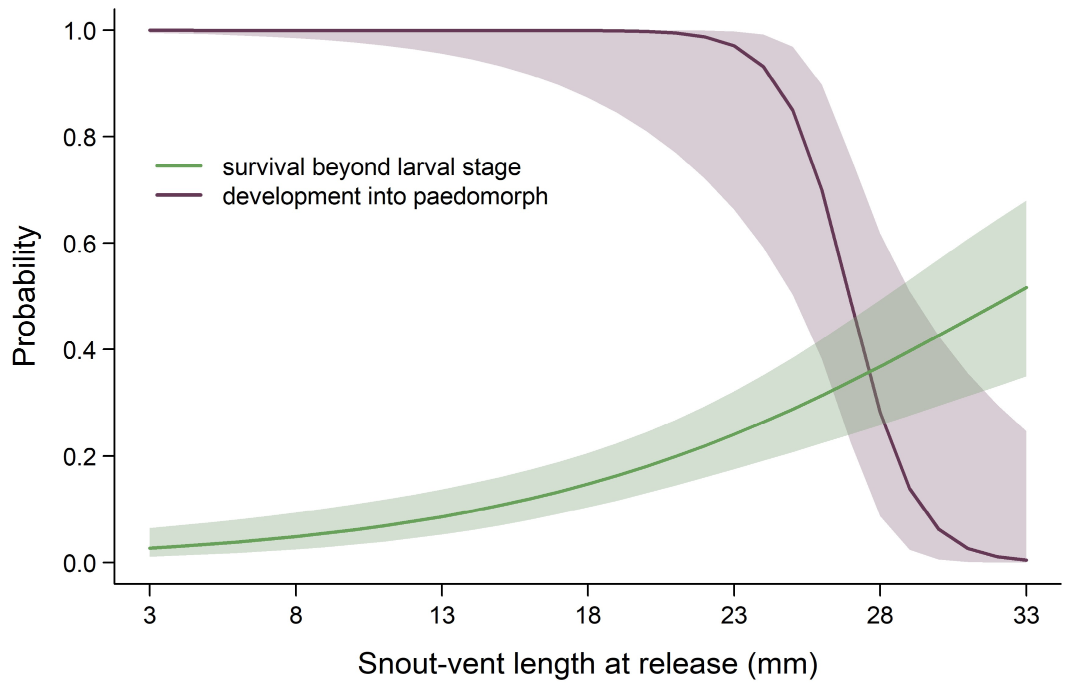

Figure 4.5. Logistic regression models of the relationship between size of captive-reared Striped Newt larvae at release and probabilities of post-release survival and development into a paedomorphic adult. While survival to the end of the larval stage consistently increases with larval size at release, maturation into a paedomorphic adult is most likely among surviving larvae released by ~22 – 23 mm snout-vent length. The probability of transitioning directly into that mature form declines dramatically for newts reared in captivity through more of their larval growth, with those individuals likely to complete metamorphosis into the highly aquatic yet gill-less and immature subadult stage.

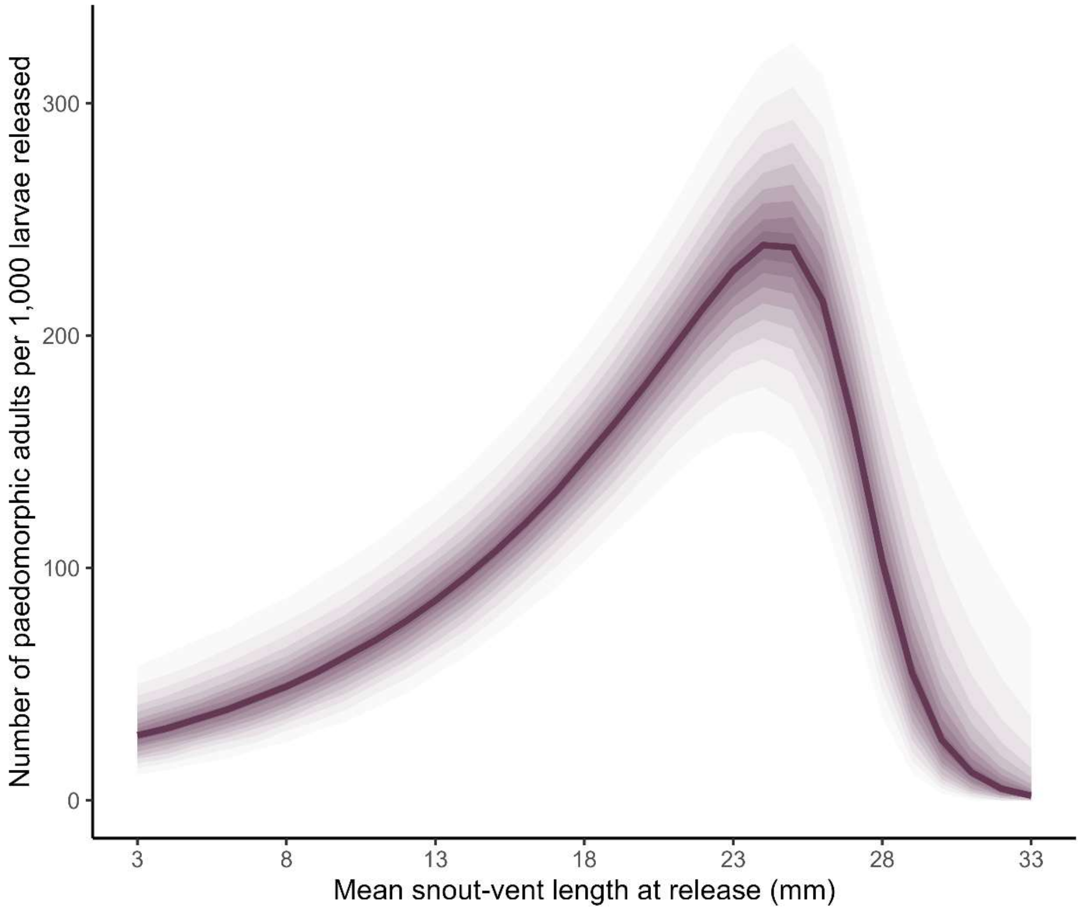

Figure 4.6. Estimated number of paedomorphic Striped Newts produced per 1,000 captive-reared larvae released, as a function of larval snout-vent length at time of release to wetland enclosures. The solid line represents the median estimate; each shaded ribbon represents a 5% confidence interval band from 5% to the 95% confidence interval based on 100,000 simulations per larval release size. Releasing larvae at 24 mm SVL is projected to produce the highest median number of individuals that survive and develop into paedomorphic adults.

CHAPTER 5

A PILOT MESOCOSM PROPAGATION EXPERIMENT TO IMPROVE DEVELOPMENTAL OUTCOMES FOR CAPTIVE-REARED STRIPED NEWTS[6]

[6]Navis, C. J. and J. C. Maerz. To be submitted to *Herpetological Review*.

Abstract

Captive propagation is an increasingly popular strategy for amphibian conservation worldwide. In the southeastern U.S., numerous entities are engaged in captive rearing of Striped Newts, a rare and declining species endemic to the region, with the goal of repatriation to remaining suitable habitat. Repatriation populations of captive-bred newts have not seen expected growth, and there exists little documentation of potential factors behind released animals' failure to readily establish self-sustaining breeding populations. Recent research points to current captive husbandry conditions reducing the likelihood that larval Striped Newts will develop into mature, paedomorphic adults as a potential cause of limited repatriation success. In an effort to mitigate the consequences of *ex situ*, laboratory captive rearing on newt development, we piloted outdoor mesocosm rearing of Striped Newts as part of a broader study of post-release outcomes for captive-reared larvae. Adult newts were allowed to breed in outdoor mesocosms, males were removed, and females were left present with their eggs and hatchlings. Despite early observations of egg deposition and hatching, we collected relatively few surviving larvae from the mesocosms and many larvae underwent full metamorphosis into other immature life stages before they could be collected at target sizes for release into *in situ* enclosures in the natural source wetland. The causes of different developmental outcomes across captive and natural environments remains unknown. We discuss potential mechanisms and highlight the importance of evaluating the conditions of captive husbandry and documenting unexpected outcomes to facilitate ongoing adaptation of captive propagation protocols.

Introduction

Serious amphibian population declines have been documented worldwide (Stuart et al. 2004, Grant et al. 2019, Luedtke et al. 2023). In response, captive propagation has become an increasingly popular strategy to establish captive assurance colonies or produce animals for release to the wild (Tapley et al. 2015, Della Togna et al. 2020). Of captive propagation initiatives that have released amphibians in an effort to supplement or repatriate wild populations, the majority appear unsuccessful in achieving conservation objectives or outcomes remain uncertain (Germano and Bishop 2009, Miller et al. 2014). Ensuring that animals reared in captivity remain well-adapted to thrive in their natural environments is challenging for most taxa due to insufficient data on the potential consequences of captive propagation—whether expressed on an individual basis (e.g., abnormal development or loss of natural behaviors) or on a population level (e.g., breeding of genetic lineages not well-adapted to the release environment) (Mathews et al. 2005).

In the southeastern United States, Striped Newts (*Notophthalmus perstriatus*) are a species with the potential to benefit from captive propagation, and emblematic of the many challenges of getting captive husbandry right. The species is endemic to southern Georgia and north/central Florida, but has disappeared from large swaths of this range (Farmer et al. 2017). Both Georgia and Florida now classify the species as Threatened (Georgia Department of Natural Resources 2017, Florida Fish and Wildlife Conservation Commission 2022). Striped Newts have been extirpated from many previously documented breeding wetlands, some of which no longer remain as suitable habitat, and researchers have noted substantial declines in many remnant populations over recent decades (Dodd and LaClaire 1995, Franz and Smith 1999, Means et al. 2008, Farmer et al. 2017). Those persisting populations are highly isolated from one another and often depend on a single breeding wetland, meaning there is seldom opportunity for natural gene flow or recolonization after population failure (Farmer et al. 2017). This makes the species a compelling candidate for management via translocation of newts to repatriate suitable habitat or for supplementation and genetic management of extant populations. Since 2011, numerous entities have collaborated to breed Striped Newts in captivity to produce offspring for repatriation (Means et al. 2011). However, the longest-running of such initiatives have yet to see population results on the scales or timelines anticipated (R. Means, pers. comm.) and it is unclear why repatriation efforts have had little success.

The highly complex life cycle of Striped Newts contributes to the challenge of rearing the animals in captivity without unintended consequences for post-release fitness (Tapley et al. 2015, Chapter 4). The species is facultatively paedomorphic; aquatic larvae can metamorphose into terrestrial, juvenile efts before eventually maturing (after potentially several years) and returning to a wetland to breed, or they can remain in aquatic form and develop directly into a sexually mature, paedomorphic adult (Mecham 1967, Johnson 2005). These alternative ontogenies are influenced by both genetics and environment, with the tendency to complete metamorphosis or develop as a paedomorph likely varying among locally-adapted populations (Wilbur and Collins 1973, Semlitsch et al. 1990, Harris et al. 1990, Newman 1992, Takahashi and Parris 2008, Levis and Pfennig 2019). A third developmental pattern of metamorphosis into a subadult form that remains highly aquatic (i.e., does not apparently undergo skin changes or emigrate terrestrially but loses its gills) is sometimes expressed in captive-reared Striped Newt larvae (see Chapter

4). This form has not been documented to occur in natural Striped Newt populations. These immature life stages cannot quickly contribute to population growth after release; thus there is interest in reducing the impacts of captivity on larval development and encouraging natural patterns of phenotypic plasticity.

In Chapter 4 we found evidence that rearing Striped Newt larvae in captivity for extended duration can irreversibly trigger metamorphic developmental pathways. Even if fully gilled at release, individuals released late as larger larvae are more likely to undergo metamorphosis into a sexually immature subadult or eft form than to mature directly into a paedomorphic adult (Chapter 4). Thus, conditions experienced during the early larval period appear to strongly influence the eventual developmental pathway. This information can inform targeted timing of larval releases to mitigate common effects of captive husbandry practices on Striped Newt life history and conservation objectives. We sought to test modifications to husbandry protocols to provide larval newts with more natural conditions afforded in large outdoor mesocosms. We expected that rates of successful mating, egg laying, and hatching would be equivalent or better to outcomes observed among Striped Newt breeding in indoor, laboratory conditions. We expected that larvae produced and reared in outdoor mesocosms would exhibit greater propensity to develop into paedomorphic adults after release into enclosures in the source wetland (see Chapter 4). Here we present the results and observations from that pilot experiment.

Methods

Mesocosm design

Polyethylene stock tanks (approx. 1135 L) were installed with approximately 2/3 of their depth below ground level in Whitehall Forest (Athens, GA). We anticipated the surrounding soil would help stabilize water temperatures year-round. Because Striped Newts are reportedly sensitive to chlorine (Means et al. 2014); we filled tanks to ground level with municipal water and allowed the water to age for a minimum of seven days. We also used commercially available water testing kits (Mars Fishcare Inc., Chalfont, PA; Jilin Hongsheng Biological Engineering Co. Ltd., Changchun, China) to monitor chlorine concentration and other water quality measures prior to the introduction of newts. Within 3 days of filling, total chlorine concentration declined to 1 ppm and pH was consistently between 6.2 - 6.8. Additional tanks filled naturally with rainwater before introduction of newts. A floating analog thermometer (extending ~16.5 cm below water surface) was placed into a tank and water temperature periodically recorded to monitor for any extreme temperature fluctuations. A HOBO temperature logger (Onset Computer Corporation, Bourne, MA) was weighted and placed into a tank for later analysis of water temperatures at tank depth. We compared mesocosm water temperatures to daily minimum and maximum air temperature data (NOAA NowData records from the Athens Ben Epps Airport weather station, approx. 7 km from the mesocosms).

We added artificial vegetation to each tank for cover and egg deposition. We also added “hides” (rectangles of corrugated plastic affixed to rocks) for adults or larvae, and floating surfaces for rest or egress of any larvae transforming into efts. The rim of each tank was lined with an ~5 cm barrier of tape overhanging the interior to prevent metamorphic newts from climbing out (backed with additional tape to prevent animals becoming trapped on the underside). To prevent invasion by local anurans and predatory invertebrates (e.g., dragonfly nymphs), we initially covered each tank with double-layered wildlife netting, held taut to the tank edges by bungee cords staked to the ground.

These covers did not prove sufficient to prevent access by anurans, so we later replaced them with mosquito netting taped to the tank rims and staked with bungee cords at one untaped end to allow researcher access. As air temperatures increased in late spring, 75% light-blocking shade cloth was added over approximately 75% of each tank to limit direct solar radiation and daily water temperature extremes. We regularly supplied tanks with live blackworms (*Lumbriculus variegatus*), and they became naturally colonized with other small aquatic invertebrates (e.g., *Daphnia* spp. and *Notonecta* spp.—although the latter is not likely prey for newts) prior to the change in cover material. Once hatchling larvae were observed or expected to be present in mesocosms, we added freshly-hatched brine shrimp every 1-2 days.

Pilot larval cohort

The first outdoor mesocosm was stocked with 21 larvae produced in our indoor facility as part of related captive propagation research (see Chapter 4 for additional details). Larvae were marked with individual VIE color combinations and moved to an existing, rainwater-filled standing outdoor stock tank on 17 November 2021 while preparations of the in-ground mesocosms were completed. All came from the same "clutch" and at that time were an estimated 159.67 ± 1.87 (mean ± SE) days old. The larvae were 30.81 ± 0.33 mm snout-vent length (SVL) and 1.29 ± 0.03 g wet mass. All the larvae retained external gills (69.0 ± 3.58 estimated percent of "full"; we considered gills extending ~8 – 10 mm as "full" based on our observations of wild and captive larvae and paedomorphs). None showed signs of sexual maturity. On 1 December 2021 they were transferred together to an in-ground mesocosm. These larvae were periodically recaptured (approx. every 46 days) to monitor survival and development until 17 April

2022, at which time they were collected for release into field release enclosures (see Chapter 4).

Mesocosm breeding and larval rearing

Beginning 19 December 2021, 13 adult Striped Newts were transferred from our indoor captive propagation colony to six outdoor mesocosms. We stocked each tank with a mature female and a mature male (with one tank receiving a second male). We attempted to reduce biasing results with known successful breeders by moving the second-most productive female from the prior breeding season to an outdoor mesocosm while leaving the most-productive 2021 female indoors (Chapter 4). Adults that had not produced young in 2021 were divided equally between the indoor and outdoor breeding settings.

Artificial vegetation in the mesocosms was checked regularly for the presence of eggs. Adult cannibalism of larvae is a potential risk, particularly within confined systems; however, some research indicates adult female salamanders can recognize their offspring, more often cannibalizing unrelated conspecific eggs (Tóth et al. 2010) or neonates (Gibbons et al. 2003). Research also demonstrates kin recognition among other salamander life stages (such as among aquatic larvae, e.g., Walls and Roudebush 1991, Pfennig et al. 1994, Harris et al. 2003, Markman et al. 2009, Berkowic and Markman 2019). We are not aware of any research examining offspring recognition by adult male caudates. Therefore, after observing that a female had begun oviposition, we began efforts to remove the adult male(s) from the mesocosm. To avoid disturbing vegetation with deposited eggs (e.g., via active dipnetting of the tanks), we used plastic minnow traps (modified by covering the sides with nylon panty hose to limit the escape of small

Striped Newt males through gaps) containing a glow stick to trap adult males overnight; we also opportunistically captured some males observed while active. Adult males were transferred to their own mesocosms with one or two other males or added to mesocosms of females that had not yet begun oviposition, to encourage successful mating. We were able to transfer all but one male out of the breeding mesocosms prior to the estimated or observed start of larval hatching.

Larvae were captured opportunistically to measure growth and development or for release into experimental wetland enclosures as part of the study reported previously (see Chapter 4). We would frequently see larvae in the tanks before they had reached target sizes for transfer to enclosures, and they could be readily captured with a small net. We captured some larvae by deploying the minnow traps overnight (modified as described above). Any larvae not already captured were retrieved at the conclusion of this experiment (10 – 19 August 2022) when we emptied the tanks of water to ensure all newts had been detected and to transfer remaining larvae to field release enclosures.

Results

We were unable to retrieve data from the temperature logger at tank depth due to unknown device malfunction. Near-surface water temperatures generally fell within the daily air temperature range reported at Athens Ben Epps Airport (Figure 5.1). On no dates did we observe water temperature colder than the daily low temperature, but on several dates we measured water temperatures that exceeded the daily high air temperature.

All 21 larvae in the initial pilot cohort survived, and by time of release had grown to 32.5 ± 0.22 mm SVL and 1.54 ± 0.04 g wet mass. Two had nearly fully resorbed gills, with one of those showing signs of maturity as a metamorphic adult male and one categorized as a subadult of unknown sex. Both of those individuals had shown substantial gill reduction prior to transfer into the outdoor mesocosm (approx. 30% of full gills). The remaining 19 had full external gills, with several individuals demonstrating regrowth of gill tissue from as little as ~45% of full gills at the time they were transferred outdoors. All of those 19 newts had swollen cloacae, a reliable indicator of sexual maturity, and were considered paedomorphic adults (Johnson 2001). We could confirm that two individuals were male by the presence of faint keratinized toe tips, but we could not confidently determine the sex of the remaining 17 individuals. While tentatively categorized as female, given that the two identified males were early in development of secondary sexual characteristics it is possible that some of the others were likewise males just reaching maturity and not yet exhibiting those traits.

We first observed eggs in the mesocosms housing adult pairs on 9 March 2022 and first detected larvae on 22 April 2022, capturing at least 14 recent hatchlings (estimated 8-12 mm total length, TL) in a single sweep with a fine mesh hand net. We observed eggs in five of the six breeding mesocosms but later detected larvae in only three of those tanks. In one of the mesocosms where we never detected larvae, we were able to promptly capture and remove one male after first detection of an egg; we were unable to capture the second male present in that mesocosm, and he remained in the tank until it was drained in early August. In the one mesocosm where we never detected eggs, the female was last observed on 20 May but was not present when the tank was drained in mid-August; it is unknown if she had mated prior to the removal of two males from the tank in late March.

In total we retrieved 21 juveniles from three mesocosms (Table 5.1). Nine already had completely or substantially reduced gills at the time of capture, and these were often detected floating near the surface of the water; none were observed using provided floats or attempting to climb tank walls. After transfer to indoor aquaria, one of those proceeded to leave the water as a terrestrial eft, while the other eight remained aquatic subadults. The other twelve juveniles retrieved from mesocosms were still in the larval stage, with full or nearly-full external gills. We observed no apparent difference in developmental stages between mesocosms; each of the three sibships included both larval and metamorphic (i.e., subadult and/or eft) juveniles. Likewise, we detected no temporal pattern in larvae retaining gills or transitioning into a metamorphic juvenile stage. Newts removed from mesocosms as larvae averaged 0.94 ± 0.09 g wet mass and 27.75 ± 1.22 mm SVL. Larvae that had begun or completed metamorphosis into subadult or eft stages by the time they were retrieved from mesocosms averaged 0.68 ± 0.09 g wet mass and 28.57 ± 0.81 mm SVL. Eleven larvae and one subadult produced in the mesocosms were released into wetland enclosures as part of our study of post-release outcomes among captive-reared larvae (Chapter 4); one mesocosm larvae died between collection and transport. During sampling of release enclosures, we eventually recaptured four of those eleven larvae after they had transitioned into a subsequent life stage. Two individuals developed into immature subadults, one developed into a fully metamorphic adult male, and one developed into a paedomorphic adult male.

Discussion

The low number of larvae produced in the mesocosms, and the still smaller subset whose ongoing development we were able to track via recapture from wetland release enclosures, limit our ability to draw many strong conclusions about the relative developmental consequences or benefits of outdoor mesocosms for Striped Newt captive rearing. However, the propagation outputs of this pilot study provide some preliminary information about the potential for outdoor breeding and rearing to meet captive-breeding program objectives and generate ideas for ways to improve and test modified approaches to captive husbandry practices.

Larval production per female in the outdoor mesocosms was slightly lower than among females in our indoor facility. In the same breeding season, four females housed in indoor aquaria produced 28 hatchlings (see Chapter 4). However, a greater proportion of the mesocosm-housed females began oviposition; in both seasons of indoor captive breeding, most females never deposited eggs, with a few relatively productive females accounting for the majority of offspring (Chapter 4).While we could not document the exact number of eggs deposited per female in the outdoor mesocosms, from our observations of egg abundance on artificial vegetation it appeared that females who began oviposition in mesocosms produced eggs at similar or higher rates relative to female newts housed indoors during the same period. We thus do not suspect that mesocosm conditions resulted in lower rates of mating or oviposition. Eggs may have hatched at low rates. In 2022 egg hatch rates in our indoor breeding facility were substantially lower than they had been the prior year (40% in 2022 versus 84.8% in 2021; Chapter 4); adults in both indoor and outdoor settings were demographically similar (i.e., age and time in captivity). It is not possible for us to know if most clutches in mesocosms had similarly low hatch rates or if larval survival was low. However, our understanding of factors commonly affecting reproductive success in pond-breeding amphibians and those previously documented in captive (laboratory) Striped Newt breeding programs suggest possible explanations. These include abiotic water conditions reducing egg or larval survival; cannibalism of eggs or young larvae (by adults or larger siblings); food limitation; depredation by intruding predators; disease; and direct UV exposure. We explore each of these potential explanations below.

Abiotic aquatic conditions. It is possible that abiotic mesocosm conditions contributed to lower hatch rates or reduced survival of hatchling larvae. In addition to likely differences in aquatic parameters between the mesocosms and Striped Newt natural breeding environments, extant breeding wetlands inarguably provide greater area and diversity of microhabitats that may support the survival of young larvae by allowing sensitive larvae to seek out optimal conditions, e.g., in regards to water temperature, light exposure, etc. as well as providing refugia from aquatic predators. During the period in which we manually recorded mesocosm water temperature, it rarely exceeded daily maximum air temperatures and was within the range of water temperatures that Striped Newts might be expected to encounter in their natural environment. Water temperature in small ephemeral wetlands can fluctuate substantially, roughly tracking daily air temperature changes (Black 1976). Such wetlands also often exhibit substantial temperature stratification in the water column, particularly when there is little wind mixing of water (e.g., as much as 10 °C difference over ~18 cm from wetland surface to bottom) (Black 1976). Unfortunately, we were not able to access the fine-timescale water temperature data at tank depth that we had hoped to collect. However, we would expect increased stability of water temperatures at tank depth and a resulting gradient of temperatures accessible to larvae for thermoregulation. Further field and experimental research would be needed to ascertain the effect of water temperature patterns on Striped Newt larval survival.

Cannibalism and food limitation. Cannibalism among amphibians is a well-documented phenomenon, with both adults and other larvae known to cannibalize larvae in a number of salamander species (Pfennig et al. 1994, Walls and Blaustein 1995, Wildy et al. 1998, Kishida et al. 2015, Berkowic and Markman 2019). While we anticipated low risk of maternal cannibalism, maternal recognition of offspring has most often been researched in species with egg-guarding maternal care (Gibbons et al. 2003) and when both related and unrelated eggs or neonates are available as prey items (Gibbons et al. 2003, Tóth et al. 2010). However, females in those studies were not presented with other food sources during the experimental period, and while they preferentially consumed unrelated eggs or juveniles, they also consumed their own eggs or offspring when unrelated options were not similarly available. In our study, females had continuous access to other food sources. Blackworms were regularly provided and we observed them surviving and persisting in abundance within the mesocosms. The mesocosms were also naturally colonized by a variety of small aquatic invertebrates, and invading frogs laid eggs that would be an additional food source at times. Food limitation thus should not have been a driver of maternal cannibalism on eggs or larvae. While cannibalism among Striped Newt larvae has been documented in aquaria captive propagation programs (Means et al. 2014), we saw no indications of cannibalism at the densities at which we housed our larvae indoors (Chapter 4). Even if hatch rates in mesocosms were high, the substantially larger mesocosm volumes would result in lower overall larval densities than in our indoor aquaria; there is no apparent reason they would cannibalize siblings rather than feed on other prey sources available within mesocosms. Kin recognition has been documented in a number of salamanders with documented larval cannibalism. In species with distinct cannibal larval morphs, these more often develop in the presence of unrelated intraspecific larvae (Pfennig and Collins 1993, Michimae and Wakahara 2001), and cannibalistic larvae preferentially select other prey when available rather than depredate siblings (Walls and Roudebush 1991, Pfennig et al. 1994). The lack of larvae (and apparent loss of eggs, following initial detection) observed in the one mesocosm with a male remaining may represent an instance of a (parental or non-parental) male cannibalizing eggs, though again the constant availability of invertebrate prey leads us to consider it as likely that the female simply deposited few, infertile or non-viable eggs.

Invertebrate predators. Colonizing invertebrate predators present another possible source of egg or larval depredation. Our initial mesocosm covers did not exclude all invertebrates, though during the oviposition and early hatchling periods we saw only small, non-predatory invertebrates (e.g., *Daphnia*) and size-limited predaceous aquatic invertebrates such as backswimmers (*Notonecta* spp.). Backswimmers typically hunt small invertebrates, spending most of their time as ambush predators on the water's surface (Miaud 1993, Martín and López 2004). In tadpole predation experiments they were limited to consuming the smallest tadpole size classes (Cronin and Travis 1986, Henrikson 1990), though hatchling Striped Newts would likely fall within their prey size range. In our observation, small Striped Newts larvae almost exclusively remain at the bottom of the water column in indoor aquaria; larger (e.g., visually detectable) larvae in the mesocosms were most often observed resting on and among submerged artificial vegetation, walking or resting on the tank floor, or swimming well below the surface. In a study in which the eggs of *Triturus* newts were offered to multiple potential invertebrate and predators, only adult newts and predaceous diving beetles (family Dytiscidae) depredated eggs while backswimmers (*N. glauca*) did not (Miaud 1993). We observed dragonfly activity near the mesocosms only later in summer, after the mesocosms were covered with mosquito netting; however, dragonflies were apparently able to deposit eggs in at least one mesocosm, as we observed several dragonfly exuviae on the underside of the mesocosm cover in mid-August. We had observed developing Striped Newt eggs in that mesocosm but never detected newt larvae. Dragonfly larvae are well-documented predators of aquatic amphibian eggs and larvae, and have been observed to be particularly effective predators of newt eggs (*Triturus* spp.) that are not enfolded by vegetation (Miaud 1993, Orizaola and Braña 2003). It is plausible that their presence prevented any newt eggs from surviving in that mesocosm. Additionally, fishing spiders (*Dolomedes* spp.) were occasionally observed in or near mesocosms. We promptly removed fishing spiders, but it is likely we did not always detect them when present. While the importance of fishing spiders as a predator of aquatic salamanders has not been well-documented, there are some case reports of *Dolomedes* spiders consuming aquatic salamander larvae (Guarisco 2010, Crane and Mathis 2015).

Vertebrate predators. Potential vertebrate predators that might have gained access to the mesocosms include snakes, Eastern Newts, and anurans. We have no indication that snakes entered any of the mesocosms. Likewise, we observed no Eastern Newts; we would have detected them if they had invaded, as their egress from mesocosms would have been blocked by the same edge barriers that ensured the Striped Newts were contained. Particularly before the change to mosquito netting covers, anurans constantly colonized the mesocosms. This occasionally included adult American Bullfrogs (*Rana catesbeiana*), which have been observed to depredate adult Eastern Newts in both captive and field experiments (Hurlbert 1970, Marion and Hay 2011). If vertebrate predators were an important factor, we would expect to observe losses of adult newts in addition to larvae.

Disease. A perhaps more pressing concern from the invasion of local wild anurans is the potential for introduction of amphibian pathogens. Common pathogens of concern for amphibians in the southeastern U.S. include *Batrachochytrium dendrobatidis* (*Bd*) and *Ranavirus* (*Rv*). *Bd* is known to cause morbidity and mortality in many anuran species and is known to be present in nearby ponds within Whitehall Forest where our mesocosms were located (C. Hazelrig, pers. comm.). Eastern Newts and Striped Newts are known to persist in wetlands with *Bd* present and infecting anurans, themselves absent of or carrying sub-clinical infections with the fungus (Rothermel et al. 2016; Hartmann et al. 2022). We have seen that under conditions favoring continued *Bd* growth, adult Striped Newts can experience mortality (Chapter 7); however, we saw no mortality among mesocosm-housed adult newts during the cooler months that favor *Bd* growth (Hartmann et al. 2024) and we would not expect that *Bd* would be a significant driver of larval attrition during the hotter months and with lower infection rates typically seen in pre-metamorphic amphibians (Hartmann et al. 2022).

Rv is a known cause of mortality among wild *Notophthalmus* (Rothermel et al. 2008, Hartmann et al. 2022). In research to assess Striped Newt susceptibility to *Rv*, nearly all metamorphs experimentally exposed to one of three *Rv* strains became infected and on average 80% succumbed to each strain. However, a minority of larvae exposed became infected and mortality was even lower (15% of those exposed to one of the strains died) (Means et al. 2012). Additionally, we observed no *Rv*-associated morbidity or mortality among adults in the mesocosms; we consider it unlikely that *Rv* had been introduced or was a factor in the low production of surviving larvae.

UV exposure. Exposure to direct UV radiation may have been a cause of egg failure or of developmental deformities that resulted in low rates of post-hatch survival. Laboratory and field studies show UV exposure can damage amphibian embryos and increase embryonic mortality, though sensitivity can vary depending on environmental conditions and among species (Licht and Grant 1997, Blaustein et al. 1998, Blaustein and Belden 2003). Experimental manipulations of *Triturus marmoratus* newt eggs unwrapped or wrapped by vegetation and exposed to varying amounts of UV radiation showed a strong effect of direct UV exposure on embryonic survival and development (Marco et al. 2001). Eggs that were enclosed by vegetation (regardless of UV exposure) experienced similar survival to unwrapped eggs not exposed to UV radiation, while unwrapped eggs exposed to UV showed significantly higher rates of embryonic developmental abnormalities and practically none survived in laboratory conditions; among unwrapped eggs exposed to ambient UV in an outdoor wetland, likewise none survived beyond 14 days (Marco et al. 2001). Our mesocosms had limited algal growth and did not have surface or emergent plant cover as is common in natural wetlands. We did not have shade cloth or other UV-blocking materials installed over our mesocosms during the late winter/early spring periods when oviposition and early embryonic development began. We also used artificial plants that are less pliable than natural plants and may have limited the ability of females to fully wrap their eggs. Newt eggs in our mesocosms were thus likely exposed to relatively high levels of UV compared to eggs laid in natural wetlands or indoors. This may have resulted in elevated embryonic mortality, reducing overall larval production compared to laboratory conditions.

Recommendations

If undertaking outdoor mesocosm propagation of Striped Newts, we recommend taking steps to limit UV exposure from the beginning of the breeding period. This could be achieved with cover materials that limit UV penetration or the inclusion of natural or artificial floating cover plants. Additionally, we recommend providing materials for oviposition that allow females to wrap their eggs, as this can be protective against both UV damage and predatory aquatic invertebrates. This could be achieved through provision of natural submerged plants, more pliable artificial plants or other materials conducive to egg attachment and wrapping. Some researchers have had success in replicating natural aquatic plants for newt egg deposition and wrapping by providing strips of thin, flexible PVC (e.g., Miaud 1993). We had previously offered submerged strips of heavy plastic garbage bag to female newts in indoor aquaria as an additional option to plastic aquarium plants, but none appeared to prefer that substrate for egg deposition. While egg-wrapping behavior varies among newt species and eggs are difficult to observe in natural settings, a researcher conducting related research recently observed Striped Newt egg deposition on creeping rush (*Juncus repens*) that had been placed within screened wetland enclosures. Some eggs were attached to plants but not wrapped, while other eggs were fully enclosed within one or multiple leaves of creeping rush (J. Samples, pers. comm.). Whether using natural plants or artificial materials, we recommend periodically removing substrates with deposited eggs to tanks unoccupied by adults to reduce the potential for cannibalism and increase control of larval densities in mesocosms. Studies of Eastern Newts show that high larval density can increase the probability of larvae developing into terrestrial efts rather than directly into mature paedomorphic adults (Harris 1987a, Bohenek and Resetarits 2018), so experimenting with Striped Newt larval stocking densities might also improve the outcomes of outdoor rearing. To reduce predation and disease risks, we recommend using mosquito netting or fine-scale mesh for covers to prevent trespass by local amphibians or other potential vertebrate predators or colonization by predatory invertebrates.

It is vital to document not only outputs of captive rearing efforts (numbers of animals reared to release), but also partial successes and failures. Identifying factors behind failures or unexpected outcomes is important to prevent wasting resources by repeating those failures across independent programs, and for adapting and making improvements to future efforts. Capacity to produce animals for repatriation will often be a limiting factor for managers, and information on larval production, captive attrition, and the impacts of captive husbandry (see also Chapter 4) is important to inform adaptive management and decision-making related to captive propagation programs.

Table 5.1. Surviving juvenile Striped Newts produced in outdoor captive propagation mesocosms. Dotted lines separate source mesocosms and corresponding sibships. All dates are 2022. Snout-vent length, total length, mass, and life stage are at time of removal from mesocosms (complete measures were not recorded for some juveniles). Life stage denotes larva (L), eft (E), or subadult (SA).

Date removed from mesocosm	**Snout-vent length (mm)**	**Total length (mm)**	**Mass (g)**	**Life stage**	**Notes**
30 June	30	61	1.15	L	released to wetland enclosure
30 June	27	50	0.78	L	released to wetland enclosure
23 July	30	60	0.65	E	
28 June	27	54	0.53	SA	
28 June	26	52	0.54	SA	
29 June	27	51	0.46	SA	
1 July	-	-	-	SA	
10 July	-	-	-	SA	
4 August	18	48	-	L	died prior to enclosure release
17 August	33	66	1.37	L	released to wetland enclosure – recaptured as subadult
17 August	31	64	1.16	L	released to wetland enclosure – recaptured as subadult
17 August	31	60	1.20	L	released to wetland enclosure
29 June	27	53	0.67	L	released to wetland enclosure – recaptured as paedomorphic adult male
29 June	25	51	0.58	L	released to wetland enclosure
29 June	25	51	0.63	L	released to wetland enclosure
29 June	27	57	0.83	L	released to wetland enclosure
29 June	26	53	0.65	SA	
1 August	28	57	0.67	SA	
8 August	33	64	1.30	L	released to wetland enclosure – recaptured as metamorphic adult male
19 August	32	66	1.19	SA	released to wetland enclosure

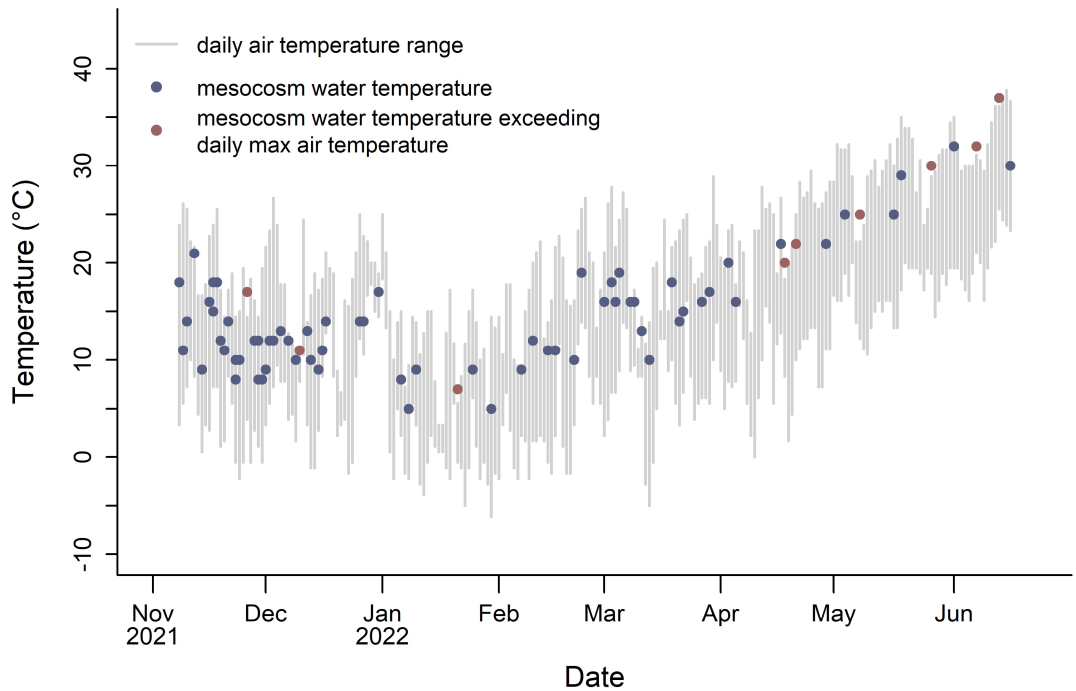

Figure 5.1. Striped Newt outdoor mesocosm water temperature and daily air temperature range. Daily minimum and maximum air temperatures are weather station readings reported by NOAA. Near-surface mesocosm water temperature readings were manually recorded between 8 November 2021 and 17 June 2022, when shade cloth was added to the mesocosms.

CHAPTER 6

DEVELOPMENT OF A POPULATION VIABILITY MODEL FOR STRIPED NEWTS TO INFORM CONSERVATION ACTIONS AND IDENTIFY RESEARCH NEEDS[7]

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Abstract

Wildlife managers often have few practical tools to guide their selection among possible management strategies and optimize progress towards conservation objectives. Population viability analysis can guide decisions by predicting population response to threats or management interventions and by facilitating identification of key life stages or life history processes to target for management. However, such models require reliable estimates of vital rates to generate meaningful projections of absolute outcomes. For many rare species, such data are not available and may be difficult to obtain. In the southeastern United States the conservation of Striped Newts is challenged by such data deficiencies, and few robust populations remain from which to gather data on vital rates. Striped Newts have a highly complex and plastic life cycle, and little is known about the survival of different life stages, transition rates between life stages, or how such rates might vary between populations. Conservation efforts focused on captive breeding of Striped Newts for release to suitable wetland habitat have largely failed to meet anticipated benchmarks of repatriation success, and recent research suggests that Striped Newt life stages commonly reared and released are not optimal for rapid population growth. Even for such a complex species with poorly-understood vital rates, a population viability model can provide insight into the relative benefit of alternate management strategies towards conservation objectives and can identify target areas for future research. We created a population viability model based on the best available data for Striped Newt population dynamics and life histories and conducted sensitivity analyses to identify the rates that most influence projected outcomes. We simulated 108 scenarios representing different management strategies and under the assumption of varying vital

rates and environmental conditions. While release of reproductively mature adults was predicted to contribute most strongly to near-term population persistence, adult Striped Newts cannot be produced reliably or without increased costs in captivity. Among strategies for the release of captive-reared larvae, releasing larvae at intermediate sizes was projected to maximize probabilities of population persistence under nearly all conditions. Sensitivity analysis showed that projections were highly sensitive to rates of adult and eft survival, frequency and effect of wetland drying, reproduction, and relative frequency of paedomorphic or metamorphic development. The simulation results we present can guide current captive rearing and repatriation decisions, while the rates highlighted through sensitivity analysis should be prioritized for data collection to continue reducing uncertainty and improving the utility of the population model.

Introduction

A key goal of wildlife ecology is to generate knowledge that reduces the uncertainty of actions and leads to better management decisions. Ecological knowledge can improve our understanding of a species' status or be used to predict changes resulting from ongoing threats or planned management actions. In the absence of practical knowledge and tools to inform decisions, management actions are often selected for ease of implementation or based on anecdotes or intuition (Crouse et al. 1987, Possingham et al. 1993, Walsh et al. 2015, Tapley et al. 2024), which may lead to undesired outcomes, failure to achieve conservation objectives, and ineffective use of limited conservation resources.

Population viability models are common tools used to guide management actions (Possingham et al. 1993, Lindenmayer et al. 1993, Brook et al. 2000, Reed et al. 2002).

Population viability analysis (PVA) can be used to compare the relative extinction risk of populations under different scenarios (McCarthy et al. 2003, Barri 2016, Boveng et al. 2018), estimate the relative influence of life stages and vital rates on population growth (Nichols et al. 2000, Wisdom et al. 2000, Zúñiga-Vega et al. 2008, You et al. 2013, Canessa et al. 2019, Ortega-León et al. 2020), and guide conservation decisions (Heppell et al. 2000, Conroy and Carroll 2009, Canessa et al. 2019, Whiterod et al. 2020). PVAs can also be useful for the management of captive breeding populations and decisions related to translocations (Faust et al. 2003, Pedrono et al. 2004, Akkoç and Williams 2005, Keating et al. 2023). To be useful, PVAs require reasonable estimates of vital rates to produce projections reliable enough to guide decision-making (Coulson et al. 2001, Conroy and Carroll 2009, Pesarakloo et al. 2020). Even for common and well-studied species, such credible rates are often not available (Beissinger and Westphal 1998, Conde et al. 2019, Howard and Maerz 2021, Christensen et al. 2024). This knowledge gap can be even more problematic for rare, understudied, or difficult-to-detect species because generating those estimates is inherently challenging while the need for action is urgent (Heppell 1998, White 2000). Where such data limitations exist, sensitivity analysis as part of PVA development can identify vital rates that most influence population projections, guiding data collection to improve model reliability and management interventions targeting influential population processes (Biek et al. 2002, Christensen et al. 2024).

Within the southeastern United States, Striped Newts (*Notophthalmus perstriatus*) are representative of these management challenges. Striped Newts are a rare salamander species endemic to the Coastal Plain of south Georgia and northern/central Florida. The species breeds in isolated ephemeral wetlands in fire-maintained pine savannas—habitat that has been largely lost or heavily altered in recent centuries (Smith et al. 2000). Many remaining wetlands in the southeastern Coastal Plain have in recent decades seen reduced hydroperiods due to vegetative succession (Van Lear et al. 2005, Enge et al. 2014, Klaus and Noss 2016) and the regional effects of climate change (Walls et al. 2013, Chandler et al. 2016), further compromising the ability of pond-breeding amphibians like Striped Newts to persist on the landscape. Recent assessment of the species across its range revealed that Striped Newts have been extirpated from parts of the Florida panhandle and Georgia (Farmer et al. 2017). As of 2017 in Georgia, Striped Newts were known to occupy only 11 breeding wetlands distributed among five properties. Population declines appear particularly acute among the western distinct population segment (DPS), which today is represented by only a handful of extant populations in the Florida panhandle and southwestern Georgia (May et al. 2011, Farmer et al. 2017). Remnant Striped Newt populations are isolated from one another by vast expanses of intensive agriculture and other land development, preventing natural dispersal, recolonization, or ongoing gene flow between populations (Dodd and LaClaire 1995, Farmer et al. 2017).

In response to these declines, a number of entities (e.g., government agencies, zoos, and other NGOs) have focused efforts on captive propagation of Striped Newts as assurance colonies and to facilitate repatriation to suitable habitat, with particular focus on populations of the western DPS (Farmer et al. 2017, Means et al. 2017, Mendyk and Beshel 2017). However, a major barrier to developing effective strategies to recover and sustain Striped Newts is the very limited data on the species' life history and population dynamics (Means et al. 2008, Burton et al. 2012; Chapter 3). Many aspects of Striped

Newt life history are exceedingly difficult to observe in the wild and others remain understudied. Published studies of Striped Newt populations are often limited to drift fence capture of efts (terrestrial juveniles) and metamorphic adults migrating to and from breeding wetlands (e.g., Dodd 1993, 1996, Johnson 2002, 2003, Means 2007). However, Striped Newts often remain in their natal wetland and mature directly into paedomorphic adults, particularly at sites where wetlands do not dry every year (Burton et al. 2012; Chapter 3). This aquatic, paedomorphic adult form appears important for population growth, but almost nothing is known about the survival and fecundity of the two adult forms or about transition rates between these and other life stages.

Understanding the population consequences of alternate developmental forms is essential to effective implementation of repatriation initiatives or other conservation actions aimed at supporting population growth (e.g., habitat management to extend the hydroperiod of breeding ponds). In species with a high degree of phenotypic plasticity, alternate ontogenetic pathways are preserved due to the opposing selective pressures of aquatic and terrestrial life in highly unpredictable environments (Wilbur and Collins 1973, Healy 1974, Newman 1992, Ryan and Semlitsch 1998, Denoël and Joly 2000, Denoël et al. 2002, Levis and Pfennig 2019). In other words, each pathway likely benefits species persistence under certain conditions, but each form may not be equally well-adapted to the conditions of an intended repatriation site or to contributing rapid progress towards conservation objectives (e.g., short-term reproduction and population growth). This has consequences for captive-breeding and release programs because captive environments may select for individuals or favor developmental pathways that are not ideal for promoting rapid population growth or longer-term persistence at a site (Araki et al. 2007, Crates et al. 2023).

Our objectives for this chapter were to (1) develop a Striped Newt population viability model based on the best available data; (2) analyze the sensitivity of model projections to changes in vital rates; and (3) apply the model to decisions regarding target life stages and sizes of Striped Newts for release from captive breeding programs. Objective (4) was to use the development of the model to identify priorities for further ecological research to improve the model and its utility to guide management decisions. Demonstrating the utility and encouraging the use of models to guide the decisions of people working in captive breeding programs is a motivation for this work.

Methods

Model structure and assumptions

We developed a population projection based on the conceptual model of Striped Newt life history depicted in Figure 6.1. Our model[8] incorporates life stages of wild Striped Newts, including terrestrial eft and paedomorphic developmental pathways. It also allows for simulation of management inputs, i.e., releases of captive-reared animals for population supplementation or repatriation. The "subadult" developmental pathway shown in Fig. 6.1 is a frequent consequence of captive rearing conditions during key periods of larval development (see Chapter 4) but is not known to occur in Striped Newts in the wild.

[8]Model code and associated documents are available at https://github.com/Maerz-Lab/Corrie-Navis-Dissertation

We chose a stage-structured matrix model (Lefkovitch 1965), as that framework is suitable for modeling population dynamics when the characteristics of distinct life stages may be more relevant than age to population growth. The model follows a pre-breeding census structure (Okuyama 2019) with annual timesteps; all young produced in a breeding season are assumed to proceed through the larval life stage and (if surviving) transition into a subsequent life stage within the same timestep (Dodd 1994; Johnson 2005). Sexes are tracked separately throughout life stages, as transition rates vary by sex in select instances (e.g., maturation of subadults). Though survival or reproduction might differ between paedomorphic and metamorphic adults, we lacked data to inform separate vital rates of the two forms and thus treated them as a single adult stage class in our model. Likewise, we did not vary survival rates between adults and subadults. We included a density-dependent function relating larval development (i.e., maturing directly into a paedomorphic adult or metamorphosing as an eft) to larval density (Figure 6.3). While this phenomenon has not been studied in Striped Newts, mesocosm experiments examining this dynamic in Eastern Newts have demonstrated a negative relationship between larval density and probability of maturing into a paedomorphic adult (Harris 1987a, Bohenek and Resetarits 2018).

The model also includes density-dependent larval survival processes to check unrealistic population projections (White 2000). There were no published or unpublished data we could identify to reliably estimate density-dependent dynamics in natural Striped Newt populations; therefore, we based this density-dependent function on values suitable to avoid "runaway" exponential simulated growth (Figure 6.2). We centered the function around midpoints estimated from our research on post-release larval survival (Chapter 4) and estimates of adult densities extrapolated from published research on wild populations (Johnson 2002). There are likely numerous processes that might limit growth of Striped Newt populations, including density-dependent factors (e.g., disease or additional forms of intraspecific competition) and environmental stochasticity (other than the simple drying variables included here). In lieu of sufficient data to simulate those ecological dynamics with any certainty, this simplified density-dependent function serves to prevent extreme projections (White 2000). No reproduction is simulated for a timestep if there is not at least one adult female and one adult male in the population; however, the simulation proceeds to allow for the possibility of efts or subadults that will survive to mature in subsequent years and contribute to population growth. No quasi-extinction threshold (i.e., a number of total population abundance, number of adults, or number of adult females below which the population is treated as functionally extinct) is incorporated into the model.

Hydroperiod is an important factor in Striped Newt population ecology, as a breeding wetland must remain ponded for approximately 6 months to facilitate successful reproduction (Burton et al. 2012). It is also a key environmental factor impacting developmental pathways and stage transitions, as only when a wetland retains water year-round (or nearly so) can larvae mature directly into paedomorphs (Semlitsch 2002, Takahashi and Parris 2008). We included a probability of annual wetland drying and assume that no newts can remain in a gilled aquatic (larval or paedomorphic) form if the wetland dries. The model also includes a conditional probability that, in years when drying occurs, the wetland dries within the larval period (i.e., before all larvae would be sufficiently developed to transition into a subsequent life stage) and consequently reduces larval survival. Survival of adults/subadults is also reduced by an adjustment factor in years when the wetland dries, as drying not only forces them to migrate (or find temporary refugia within the wetland basin) but is often indicative of annual conditions (e.g., drought) less conducive to their terrestrial survival (Healy 1974, Dodd 1993, Carey and Alexander 2003).

Defining baseline vital rates

The full set of baseline vital rates and environmental probabilities used to parameterize the model are provided in Table 6.1, along with sources used to inform those initial parameters. Given the dearth of available data on some Striped Newt life stages or transitions, in some instances we used proxy data from closely related but better-studied species (e.g., Eastern Newts, *Notophthalmus viridescens*). To allow for stochasticity between years and populations, the model draws values for each timestep and iteration from a normal distribution around baseline parameter values. Because data are lacking on natural variation of most demographic rates, we assigned uncertainty of ± 0.025 SD to parameters that represent probabilities. Variability in reproductive rates is similarly incorporated by scaling that degree of uncertainty to the number of hatchlings per adult female (SD calculated as ± 0.025 × the baseline value).

When modeling the effect of management actions, we allowed for scenarios wherein captive-reared Striped Newts were released to a repatriation site (no extant population) or to supplement an existing population. These are the two primary approaches of current captive-breeding programs. Management scenarios may be defined as inputs of any combination of male adults, female adults, subadults (i.e., captive-reared larvae that have already transitioned to that stage prior to release), and larvae of 10 mm, 15 mm, 20 mm, 25 mm, or 30 mm SVL. Survival and maturation probabilities for each size class of captive-reared larvae were extracted from our findings on post-release outcomes for captive-reared Striped Newt larvae (Chapter 4). As with the core population vital rates, the precise value applied in each annual timestep and iteration is drawn from a normal distribution (using SD values specific to each larval size class) around the baseline probability.

Sensitivity assessment

We evaluated the sensitivity of model projections to changes in most vital rates and environmental parameters (i.e., those with a high amount of uncertainty). In each instance all other parameters were held constant at the baseline values (Table 6.1) while a single rate was varied to determine the proportional impact on the probability of population persistence to 15 years. Each value was tested with 4,000 iterations. Percent change in the parameter value and in persistence probability were calculated from the median of values used for each parameter.

We additionally assessed the sensitivity of the model to values of subadult maturation (separate probability rates for female subadults in the first year following transition into the subadult stage, female subadults in all subsequent years, and male subadults in all years). These were simulated from a starting population of zero and with release of 50 captive-reared larvae of 30 mm SVL (which have a high probability of transitioning into the subadult form) in the first year of the projection. All other parameters were held consistent at baseline values.

Simulated scenarios

We simulated alternative management approaches to repatriation (i.e., releases to a suitable wetland with no extant Striped Newt population). Scenarios included varied life stages selected for release (captive-reared larvae of 10 mm, 20 mm, or 30 mm SVL at release, or mature adults in equal sex ratios) and released in different quantities (2, 10, 20), under varying probabilities of wetland drying (0.2, 0.5, 0.8). We also varied a set of vital rates around which there is high uncertainty, adult/subadult survival (probabilities of 0.2, 0.5, and 0.8). In total we simulated all 108 combinations of these parameters with 4,000 iterations per scenario, projected to 15 years. All other parameters were left at baseline values.

Results

Sensitivity to parameter values

Persistence probability increased with rates of adult and eft survival but began to plateau at higher survival values, possibly due to the density-dependent dynamics in the model that moderate population growth (Figure 6.4). Model projections were also highly sensitive to how substantially we assume wetland drying reduces adult or eft survival (drying adjustment factor), resulting in projected persistence probabilities ranging from 0.290 – 0.920 (Figure 6.4). Increases in wetland drying led to declines in population persistence, but perhaps counterintuitively, projected population persistence was more sensitive to the absolute probability of the wetland drying than to the probability that drying would occur early enough to catastrophically reduce larval survival (Figure 6.5).

Increasing the mean number of hatchlings produced per adult female improved projected population persistence, up to a rate of 50 hatchlings/female (Figure 6.6).

Persistence probability began to plateau with further increases of mean reproductive output. Simulations using the lowest reproductive rates (5 or 10 hatchlings/female) had zero probability of persisting to 15 years or negligible likelihood of doing so (20 hatchlings/female; probability of persistence = 0.007). The probability that larvae mature directly into paedomorphs under year-round ponded conditions displayed a strong positive influence on population persistence (Figure 6.7). Eft maturation probabilities had a weaker but likewise positive effect on persistence probability (Figure 6.7). Varying rates of subadult maturation had unclear effects on persistence probabilities. Increasing maturation rates in male subadults or in females after their first year as subadults appeared to somewhat improve population persistence, although both trends displayed a good deal of variability. The maturation rate among female subadults within their first year in that life stage exhibited no clear relationship to population persistence (Figure 6.8).

Changing the amount of inter-annual variability in the model by adjusting the size of standard deviations applied to most probabilities and to the number of hatchlings per adult female, respectively, did not result in clear patterns of change in persistence probability (Figure 6.9).

Simulated management scenarios

In all scenarios, releasing a greater number of individuals improved the probability of population persistence to 15 years, although in some cases this difference was small (Figure 6.10). For example, in scenarios where larvae were released at 10 mm SVL or when subadult/survival was low, releasing larger numbers of individuals had limited effect on population persistence (Figure 6.10). Release of sexually mature adults produced the greatest probability of population persistence in most scenarios, particularly when adult survival was ≥0.5. Increased wetland drying generally dampened persistence probabilities across management scenarios, though not always dramatically. When adult/subadult survival was high and larger numbers of newts were released, wetland drying had a smaller effect on population persistence. Under nearly all combinations of parameters, releasing larval newts at 20 mm SVL was better for population persistence than releasing the same number of 30 mm SVL larvae. Under only four out of 27 conditions did releasing larvae at 30 mm SVL improve projected population persistence; however, those differences were small (0.009 – 0.035). Each occurred when wetland drying probability was moderate to high (0.5 or 0.8) and/or when high subadult/adult survival (0.8) was assumed.

Discussion

It is important to remember that this PVA cannot generate *absolute* predictions about population persistence or about the realized outcomes of a chosen management approach. A PVA such as the one we present here is most appropriately useful to conservation planning by comparing *relative* outcomes of alternative scenarios, making explicit assumptions about species life history and population dynamics, and using sensitivity analyses to identify those vital rates where additional data is needed to improve model projections (Akçakaya and Sjögren-Gulve 2000, Biek et al. 2002, Schmolke et al. 2010). The reality of conserving imperiled species is that managers are unable to wait for ideal data and must decide among alternative approaches with imperfect information and often high uncertainty (White 2000, Lawson et al. 2021, Christensen et al. 2024). Even imperfect models can be useful tools to inform that decision-making—particularly when they are limited to relatively short-term predictions, and with transparency about what answers the PVA can and cannot provide due to remaining uncertainties (Goldwasser et al. 2000, White 2000, Brook et al. 2000, Schmolke et al. 2010).

While the 108 scenarios we simulated represent a small cross-section of potential parameter combinations and management strategies, they provide insight into the value of using a PVA model to transparently and quantitatively weigh multiple management options and identify potential unanticipated outcomes of management interventions. Density-dependent population dynamics, environmental variability, and the complexity of life histories such as seen in Striped Newts mean that predicting the impact of a particular management strategy is anything but intuitive. Our model indicates that releasing sexually mature adults would be the most effective way to increase success of repatriations; however, at present there are no tested protocols for reliably raising captive-bred Striped Newts to reproductive maturity (Chapters 3, 4). Therefore, use of adults in repatriation efforts would most likely require translocation of wild adults from a source population to a repatriation site. Removal of adults from wild populations—for direct translocation or as additional stock for captive breeding programs—will necessitate careful consideration of adult harvest effects on source populations. Our population model can be adapted to facilitate such analysis, although a reasonable estimate of the source population size is needed for reliable projections. Until breeding adults can be produced in captivity and if the translocation of wild adults is constrained, translocation programs must rely on wild-collected or captive-reared larvae. It may seem intuitive that rearing larvae to larger sizes will improve individual post-release survival and population establishment; however, as demonstrated in Chapter 4, releasing larvae at larger sizes reduces the likelihood that those larvae will develop into paedomorphic adults capable of breeding within their first year. This is why our PVA predicts that under most of our simulated scenarios, releasing captive-reared larvae at intermediate sizes maximizes the likelihood of population persistence to 15 years despite reduced survival of those captive-reared larvae after release. Only if adult and subadult survival are exceptionally high would releasing older, larger larvae approach similar projections of population persistence. Therefore, we currently recommend that Striped Newt repatriation programs focus on releasing larvae at intermediate sizes (~20 mm) if translocation of wild, breeding adults is not viable.

Our sensitivity analyses demonstrated that low rates of annual eft or adult survival, including large reductions in adult survival during periods of dry weather that lead to wetland drying, will negatively affect Striped Newt population persistence, particularly for small repatriated or relic populations. Though little is known about adult Striped Newt survival in the wild or how it is affected by wetland drying, migration, or extended drought, these results are consistent with patterns documented in limited published field studies of Striped Newt populations. During a 5-year population study coinciding with a drought, Dodd (1993) observed a shift towards larger Striped Newts and interpreted the trend as indicative of continued growth of surviving individuals. However, only a small portion of newts marked during migration periods were ever recaptured (16.93% were recaptured after one year, less than 1% after two years, and none after four years) (Dodd 1993). This suggests that terrestrial mortality may be high during drought conditions, and that wetland drying and concurrent terrestrial drying may substantially reduce Striped Newt survival. Field collection of additional data to better estimate post-larval survival rates and understand how they are impacted by wetland and terrestrial drying would be valuable in improving reliability of model projections for conservation decision-making, including estimating the relative benefits of various management approaches. For example, if adult survival is substantially reduced when wetland drying forces them to emigrate, attempted repatriation of Striped Newt populations without attention to habitat management to improve terrestrial survival or wetland hydroperiod may be destined to fail.

It is possible, however, that Striped Newts life histories and facultative life cycles have evolved to facilitate population rebound following high mortality events associated with wetland drying and periodic droughts. Dodd and Johnson (2007) documented Striped Newts colonizing new breeding ponds after drying extirpated predatory fish, indicating that some terrestrial dispersal and recolonization does occur. They also documented several Striped Newt larvae in a small pond where none had been detected during a decade of intermittent sampling (Dodd and Johnson 2007). Such recolonization after years of insufficient hydroperiod, or colonization of newly-available breeding ponds, requires that either a) migrants from nearby breeding ponds migrate to and colonize the pond, or b) juvenile and/or adults are sufficiently long-lived in terrestrial environments to return to a pond when conditions improve (Gibbons et al. 2006, Taylor et al. 2006, Price et al. 2012). In other words, with sufficiently high survival rates, terrestrial phases of Striped Newts might function as a storage phase analogous to a seed bank that allows populations to persist through extended periods of reproductive failure. At the Florida location where Dodd and Johnson (2007) observed breeding pond colonization, Striped Newts had been detected in numerous wetlands and were believed to function as a metapopulation, with migrants likely driving (re)establishment in previously-extirpated or unoccupied breeding ponds. At locations where Striped Newts are known to breed in only one wetland, or where managers are attempting repatriation to a wetland with no extant breeding population nearby, recolonization from nearby breeding ponds cannot be depended upon if a population is extirpated. Under such circumstances, it is particularly relevant to understand stage-specific survival rates and longevity of Striped Newts in upland environments and to optimize repatriation efforts from captive-rearing and translocation programs.

Remaining gaps in knowledge

While we structured our model and defined baseline parameters based on the best available data on Striped Newt life history, ecology, and population dynamics, this model is a simplified representation of Striped Newt population dynamics using numerous unknown parameters. For some of the parameters and processes discussed below, there are no estimates of vital rates, let alone information on how those rates vary spatially or over time in response to environmental factors. Incorporating all possible life history and ecological processes and addressing the potential sensitivity of all those rates was beyond the scope of our present objectives. Nonetheless, generating estimates of those rates will be important to model some management scenarios or to make the model useful in predicting the dynamics and persistence of some managed Striped Newt populations across the species' range.

In our model, we did not differentiate between fully metamorphic and paedomorphic adults. However, evidence from other facultatively paedomorphic salamanders suggests there may be important differences in reproduction or longevity between metamorphic and paedomorphic adult forms. Specifically, in a number of facultatively paedomorphic salamander species there appear to be life history tradeoffs between short-term reproduction and longevity. Paedomorphs exhibit a "faster" life history characterized by earlier maturation and high levels of annual reproduction while fully metamorphic adults have a "slower" life history characterized by a later age at first reproduction and lower annual reproductive output but greater longevity (Rot-Nikcević et al. 2000, Winne and Ryan 2001, Lackey et al. 2019, Kirk et al. 2023, Cayuela et al. 2024). While these trends are not universal and can vary among populations of the same facultatively paedomorphic species (Kalezić et al. 1996, Rot-Nikcević et al. 2000, Denoël et al. 2002, 2005), it is well established that vital rates are typically not identical for paedomorphic and metamorphic adults within the same salamander species or population (Whiteman 1994, Denoël et al. 2009). This is an area of research that may prove very influential to projections of Striped Newt populations and on potential management decisions, given the frequent ontogenetic constraints experienced by captive-reared larvae (Chapter 4) and potential differing population contributions (i.e., short-term population growth vs. population resiliency in environments prone to drought) of the two phenotypes. We believe that differential vital rates will show that translocation of paedomorphic adults or larvae that are likely to develop into paedomorphic adults will have a larger, positive effect on near-term growth of translocated populations and therefore should be the key target for rapid establishment of repatriated populations or to supplement extremely small populations. Production and release of metamorphic adults or subadults might be a suitable target for later, secondary supplementation of repatriated populations or to increase long-term resilience of moderately sized extant populations.

In our sensitivity analyses, increasing values of some parameters improved the probability that the population would persist to at least 15 years, but that response reached a plateau. This is likely the result of inclusion of two density-dependent mechanisms in the PVA that inhibit unlimited population growth. Management actions aimed at increasing specific rates may only boost population growth to a point, depending on density-dependent dynamics in a population. Integrating density-dependent processes is important to represent realistic population dynamics, but density-dependent processes can be complex and difficult to estimate for many species (Beissinger and Westphal 1998, Vonesh and De la Cruz 2002). We lack data on actual density-dependent mechanisms and rates in Striped Newt populations, and there are likely other density-dependent processes that we did not incorporate into this model. Intraspecific competition across and within life stages are well-known density-dependent processes for aquatic amphibians (Morin 1983, Wilbur 1997). Density-dependent effects on larval growth and development can impact not only larval survival (Scott 1990) but carry over to consequences for terrestrial juvenile and adult fitness (Scott 1994, Taylor and Scott 1997, Scott et al. 2007, Vignoli et al. 2018). Density might also affect rates of metamorphosis into terrestrial forms (Semlitsch 1987, Harris 1987a, Whiteman et al. 2012, Bohenek and Resetarits 2018), with potential differences in survival and fecundity between alternative forms (Denoël and Joly 2000, Cayuela et al. 2024). In newts, density might also be negatively related to egg or larval survival through cannibalism (Harris 1987b, Wildy et al. 2001, Burlacu et al. 2009, Vaissi and Sharifi 2016, Vignoli et al. 2018), a common density-limiting mechanism in aquatic salamander populations that often interacts with interspecific dynamics or environmental conditions (Polis 1981, Kuzmin 1991, Toscano et al. 2017, Rosenheim and Schreiber 2022). Thus it is likely that density-dependent processes are more complex than currently represented in our model. Future research on density dependence in Striped Newt populations would be beneficial towards improving models of population dynamics, and should include examination of how density-dependent processes function in the aquatic and fully metamorphic life history pathways (Denoël and Joly 2000, Denoël et al. 2009).

This PVA includes probabilities of annual wetland drying and timing of drying, but these probabilities were applied similarly in every year of simulated populations. Climatic conditions may result in extended droughts resulting in consecutive years of breeding wetlands drying or failing to refill. We did not examine the relationship between experiences of consecutive years of drying or early drying and the persistence of simulated populations. While the phenotypic plasticity observed in Striped Newts likely contributes to population resilience to seasonal wetland drying and moderate periods of drought (Dodd 1993, Denoël et al. 2005), climate change is predicted to result in more frequent extreme climatic conditions. Severe multi-year droughts and rising temperatures can drive rapid declines in amphibian condition and survival of terrestrial life stages, contributing to population declines or local extinctions (Carey and Alexander 2003, Jones et al. 2017, Bucciarelli et al. 2020). The ability of facultatively paedomorphic salamanders to flexibly respond to environmental conditions may not be sufficient to buffer populations against the impact of more extreme and lengthy droughts (Davis et al. 2017), as increasing frequency of drought and resulting years of reproductive failure can threaten population persistence (Crawford et al. 2022). Consideration of the potential for extended drought is particularly relevant in relation to estimates of longevity and terrestrial survival, as terrestrial life stages must survive to restart population growth following multiple years without reproduction.

While facultatively paedomorphic species retain the flexibility to mature in either aquatic or terrestrial environments, before or after metamorphosis, this response to environmental cues is not uniform across populations. Numerous studies have shown that the propensity of facultatively paedomorphic salamanders to metamorphose varies among populations. Populations differ in their sensitivity to environmental triggers that may induce metamorphosis, indicating a genetic basis of predisposition to metamorphosis (Wilbur and Collins 1973, Semlitsch et al. 1990, Harris et al. 1990, Newman 1992, Takahashi and Parris 2008, Percino-Daniel et al. 2016, Levis and Pfennig 2019). The relative benefits of metamorphosis (such as the ability to colonize additional breeding habitat or to persist through periods of drought) depend on the local environment (Whiteman et al. 1996), with populations showing local genetic adaptation to the hydroregime of their own breeding wetland (Takahashi and Parris 2008). It is important to be aware that such differences exist among populations and that vital rates derived from the study of one population may not perfectly inform projected outcomes for another population or environment (Gurevitch et al. 2016)/ To the extent such data can be obtained, relevant parameter values should be updated based on rates calculated from the population of interest when modeling projections for that population. The potential for local genetic adaptation between Striped Newt populations is also important to consider when simulating release of captive-reared larvae sourced from one population—

particularly one with a notably different hydroregime—to an intended repatriation site. The maturation probabilities for captive-reared larvae according to size (SVL) at time of release were empirically derived from research on post-release outcomes of larvae released in the same wetland from which their parents were collected (Chapter 4), so those rates were not affected by population-level differences in rates of metamorphosis. Outcomes may differ from those projected by the model if larvae are released into an environment substantially different from that to which their lineage is genetically adapted.

While our sensitivity analysis did not demonstrate a clear relationship between population persistence and the amount of variability included in the model structure (via scale of SD assigned around mean rate values), it has been illustrated elsewhere that greater degrees of demographic or environmental variability within a population generally result in lower probability of persistence—even if undergoing mean annual population growth, small populations are more likely to experience catastrophic declines or extinction under highly variable conditions (White 2000). Obtaining additional data on key vital rates will also allow for calculation of SDs specific to those dynamics in Striped Newt populations.

Conclusions

While an imperfect representation of the real complexities of Striped Newt life history and ecology, a PVA based on limited data available for a rare species can be valuable in providing direction to ongoing conservation efforts. By being transparent about assumptions of the model structure and bases of parameter values we have aimed to present its greatest benefits—illumination of the relative benefits of management alternatives and identification of key targets for additional natural history research—but avoid the pitfalls of interpreting a PVA to have more absolute predictive power than it reliably does. This PVA is not intended to be a final representation of Striped Newt population dynamics, but a useful framework to build from and to use in directing future research that may continuously improve the reliability of its projections.

Table 6.1. Baseline parameter values used in the Striped Newt PVA.

Parameter	Value	Sources informing baseline value
Core vital rates		
proportion female	0.554	Population research (Chapter 3) (0.515) Dodd 1993 (0.594) Johnson 2002 (0.556)
number of hatchlings per adult female	50	Estimate from captive propagation (Chapter 4)
larval survival[†]	0.028	Study on post-release outcomes of captive-reared larvae (Chapter 4)
larval maturation (when wetland remains ponded)	0.9	Population research (Chapter 3)
eft survival	0.4	ǂ
eft maturation	0.25	Estimate based on range of eft period lengths reported for *N. viridescens*
adult survival (when wetland remains ponded)	0.4	ǂ
adjustment factor: proportion of adult/subadult survival, when wetland dries	0.7	ǂ
Environmental factors		
wetland drying	0.4	Wetland characteristics should be adjusted as applicable to populations or repatriation wetlands of interest; baseline values based on the hydroregime of the Striped Newt breeding wetland where we conducted most field research (Chapters 3, 4) or selected to represent intermediate Striped Newt breeding wetland size
early drying of wetland during larval period (conditional on wetland drying)	0.1	
adjustment factor: proportion of larval survival, when early drying occurs[§]	0.5	
ponded wetland area (m^2)	500	
mean wetland depth when ponded (m)	1	

(continued on following page)

Table 6.1, continued

Parameter	Value	Sources informing baseline value
Vital rates applicable in management scenarios		
survival of captive-reared larvae (10mm SVL)	0.053 ± 0.017	Study on post-release outcomes of captive-reared larvae (Chapter 4)
survival of captive-reared larvae (15mm SVL)	0.088 ± 0.021	
survival of captive-reared larvae (20mm SVL)	0.143 ± 0.027	
survival of captive-reared larvae (25mm SVL)	0.224 ± 0.045	
survival of captive-reared larvae (30mm SVL)	0.332 ± 0.076	
maturation of captive-reared larvae (10mm SVL)	0.984 ± 0.031	
maturation of captive-reared larvae (15mm SVL)	0.937 ± 0.081	
maturation of captive-reared larvae (20mm SVL)	0.781 ± 0.139	
maturation of captive-reared larvae (25mm SVL)	0.458 ± 0.128	
maturation of captive-reared larvae (30mm SVL)	0.167 ± 0.119	
subadult survival (when wetland remains ponded)	0.4	ǂ
subadult maturation (females, first year in stage)	0.1	Study on post-release outcomes of captive-reared larvae (Chapter 4)
subadult maturation (females, subsequent years)	0.25	
subadult maturation (males)	0.4	

† This value for larval survival is used only in calculation of the stable stage distribution, as larval survival relates to adult density in simulation timesteps

ǂ Selected as initial baseline values due to insufficient data to inform these rates

§ This adjustment factor is included among environmental factors as it should be adjusted based on the hydroregime and breeding phenology for a Striped Newt breeding wetland of interest

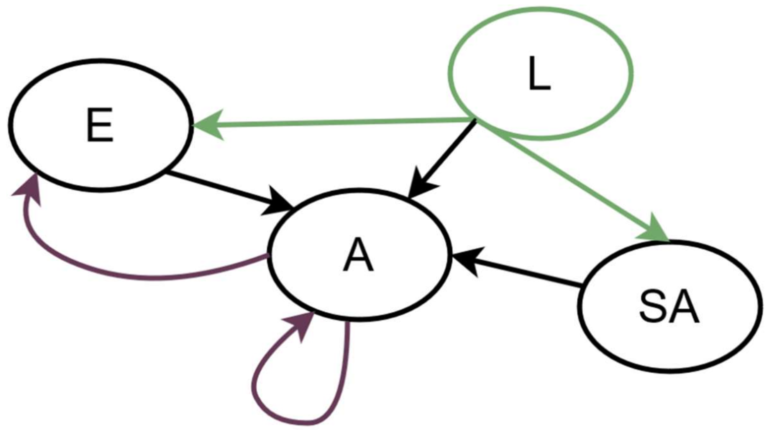

Figure 6.1. Conceptual model of Striped Newt life history reflected in the population projection model. The pre-breeding census and combined treatment of the two adult forms means that only adults (A) and efts (E) are represented in annual counts when simulating natural populations. Releases of captive-reared larvae (L) can be included to model the impact of management interventions for repatriation or population supplementation, and (like naturally-occurring larvae) transition to another stage class prior to the next timestep. Subadults (SA) are produced only as a potential outcome of management scenarios (release of captive-reared larvae or juveniles already in subadult form), though may remain in that life stage into subsequent timesteps and are tracked accordingly in the model. The number of individuals in each life stage is defined by survival rates, individuals remaining within a life stage, maturation from a juvenile to mature stage (black arrows), reproduction (purple arrows), or transition between immature stages (green arrows).

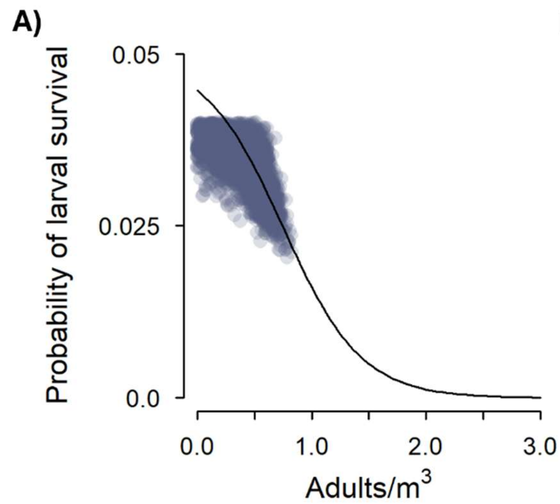

Figure 6.2. Density-dependent relationship of Striped Newt larval survival and adult density as modeled in the PVA. The line represents a best fit sigmoidal curve of four points created based on few published population studies including sufficient data for broad estimates of adult density, our research estimating larval survival (Chapter 4), and limited published data on adult densities in Eastern Newt populations. The probability of larval survival (S_L) was calculated in each timestep using the function:

$$S_L = 0.04967 \ / \ (1 + e^{(d_A\, -\, 0.7482)/0.3416} + \varepsilon)$$

where d_A represents adult density (N_A / ponded wetland volume) and ε was modeled as a Gaussian function with a = 0.18, b = 0.01, and c = 20. Larval survival was limited to a maximum of 0.04. As seen (A), adult densities are unlikely to often reach levels where this density-dependent function strongly dampens larval survival; however, inclusion of this function contributes variation in annual larval survival (B, same data with axes adjusted to show detail) and prevents unrealistic, “runaway” simulations of exponential population growth. Points are larval survival values in timestep 25 in 2,000 simulations with an initial population of 50 adults and 500 m^3 wetland volume.

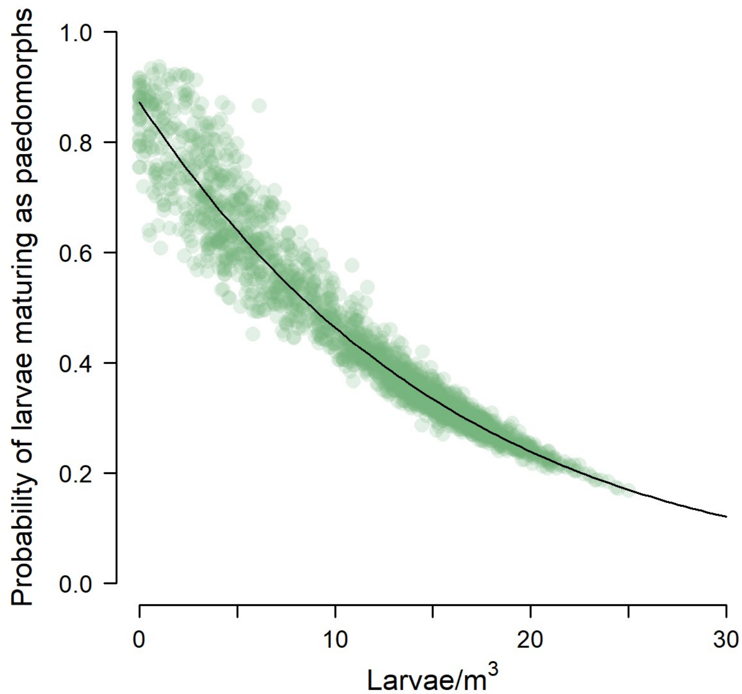

Figure 6.3. Density-dependent function relating Striped Newt larval development (probability of maturing directly into paedomorphic adult form, in years when the wetland remains ponded) to larval density. The line represents a best fit sigmoidal curve of six data points from published studies of Eastern Newt larval density and developmental outcomes, and five points created to allow calculation of the curve. The probability of larvae maturing when the wetland remained ponded (M_L) was generated for each timestep with the function:

$$M_L = 6.1758 \;/\; (1 + e^{(d_L\, +\, 25.6521)/14.2062} + \varepsilon)$$

where d_L represents larval density (N_L / ponded wetland volume) and ε was modeled as a Gaussian function with a = 1, b = 0.6, and c = 20. Points are probability values in timestep 25 in 2,000 simulations with an initial population of 50 adults and 500 m^3 wetland volume.

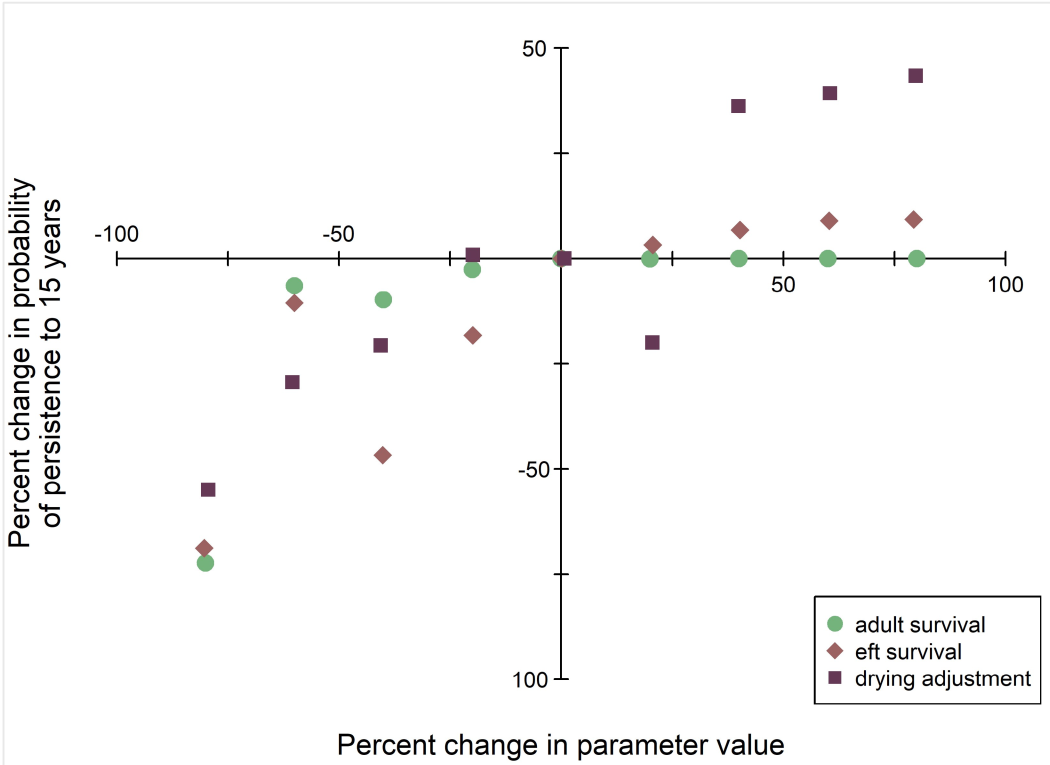

Figure 6.4. Sensitivity of model projections to changes in eft and adult survival and the degree to which wetland drying impacts adult survival. Each parameter of interest was adjusted separately while all other parameters were held constant at baseline values. Adult and eft survival probabilities were adjusted to value from 0.1 – 0.9, while the drying adjustment factor was assessed at values from 0.1 – 1.0.

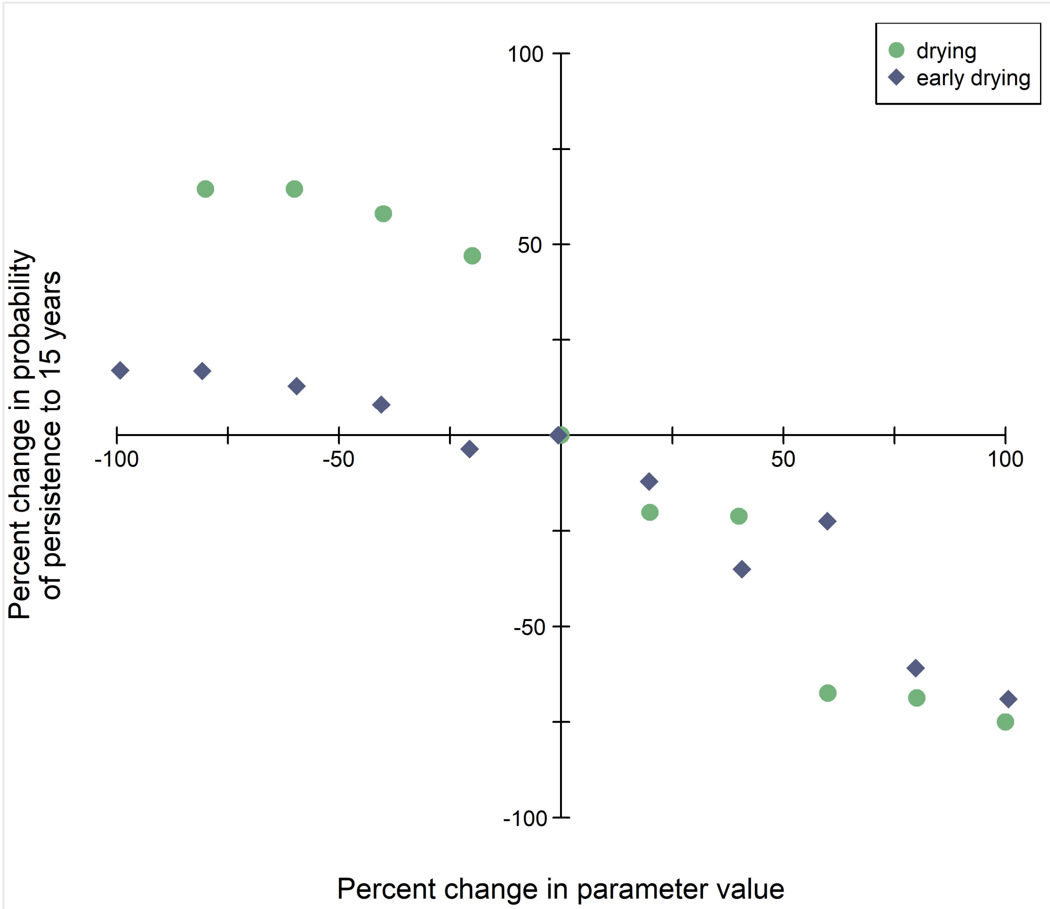

Figure 6.5. Sensitivity of model projections to changing probabilities of annual wetland drying and early drying. Each parameter of interest was separately adjusted to values ranging from 0.1 – 1.0 while all other parameters were held constant.

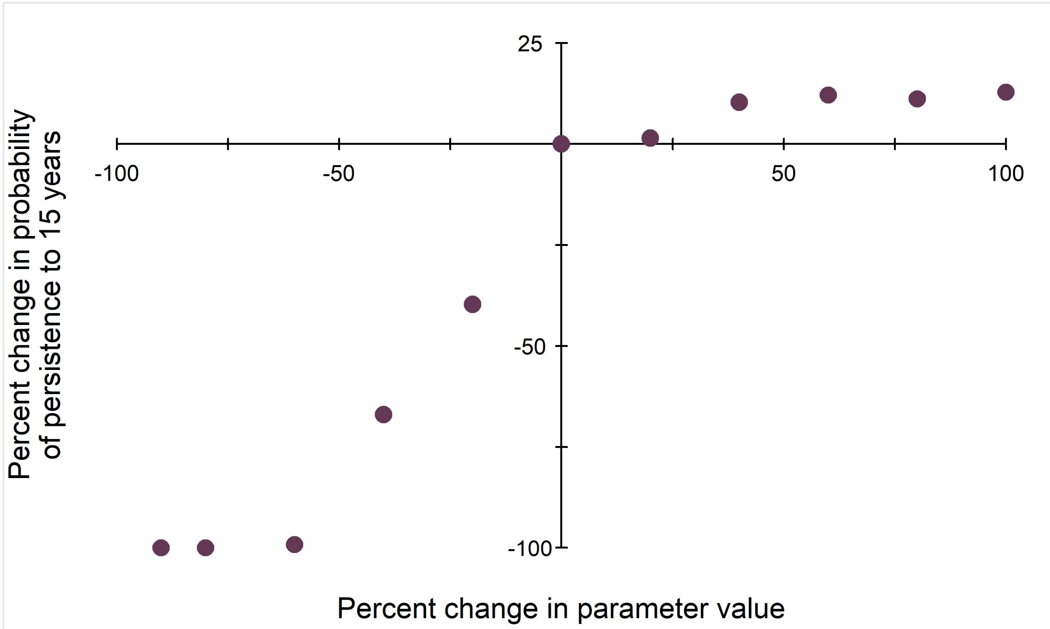

Figure 6.6. Sensitivity of model projections to changes in the mean annual number of hatchlings produced per adult female. Projections were generated for values ranging from 5 – 100 while all other model parameters were held constant.

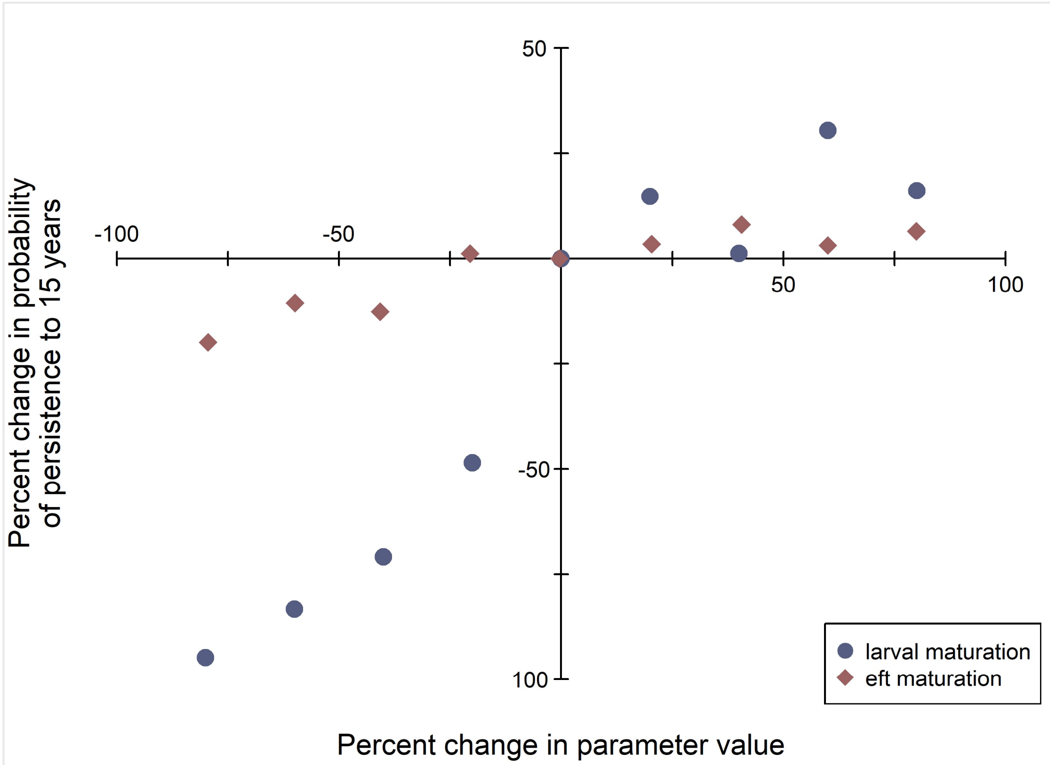

Figure 6.7. Sensitivity of model projections to changes in the probability of larvae maturing into paedomorphic adults and the probability of efts reaching maturity. Both rates were adjusted, in turn, to values ranging from 0.1 – 0.9 while all other parameters were held constant.

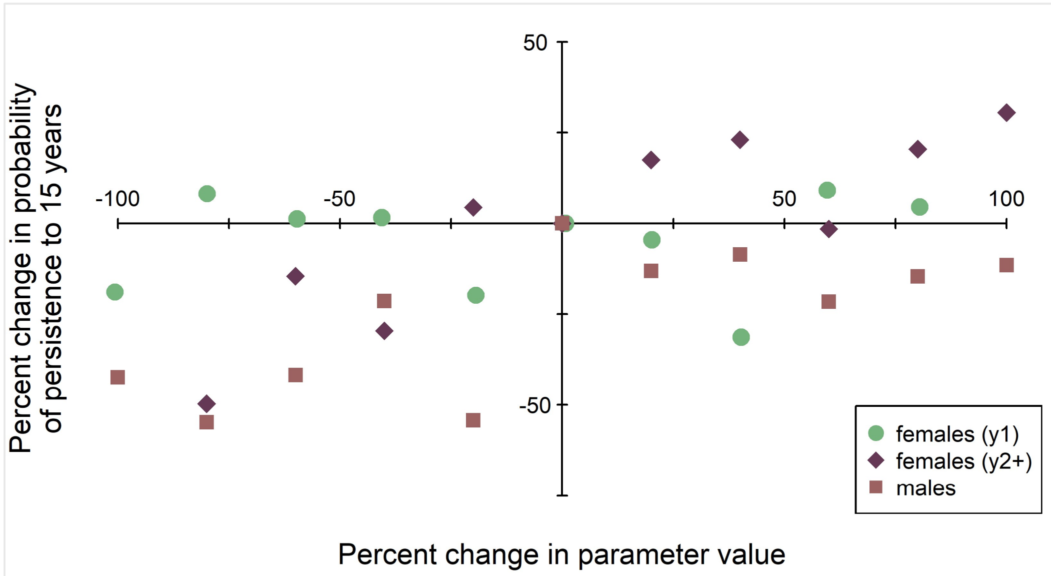

Figure 6.8. Sensitivity of model projections to changes in the probability of subadults reaching maturity. Each parameter of interest was adjusted while all other parameters held constant.

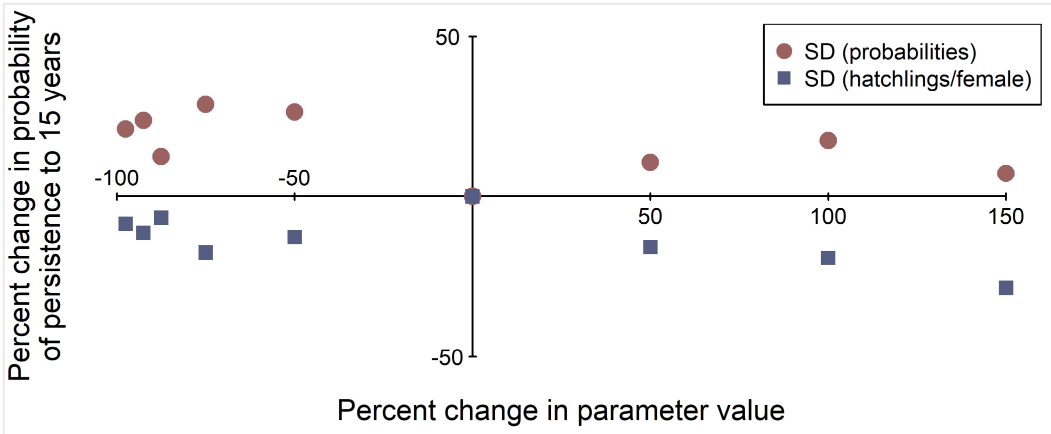

Figure 6.9. Sensitivity of model projections to changes in the amount of parameter variability between years and simulated populations. The standard deviation (SD) that defines the distribution of model parameters that are on a probability scale was adjusted to values from 0.005 – 0.25 while all other model parameters were held constant. The SD value used for the number of hatchlings produced per adult female was separately adjusted to values from 0.25 – 25.

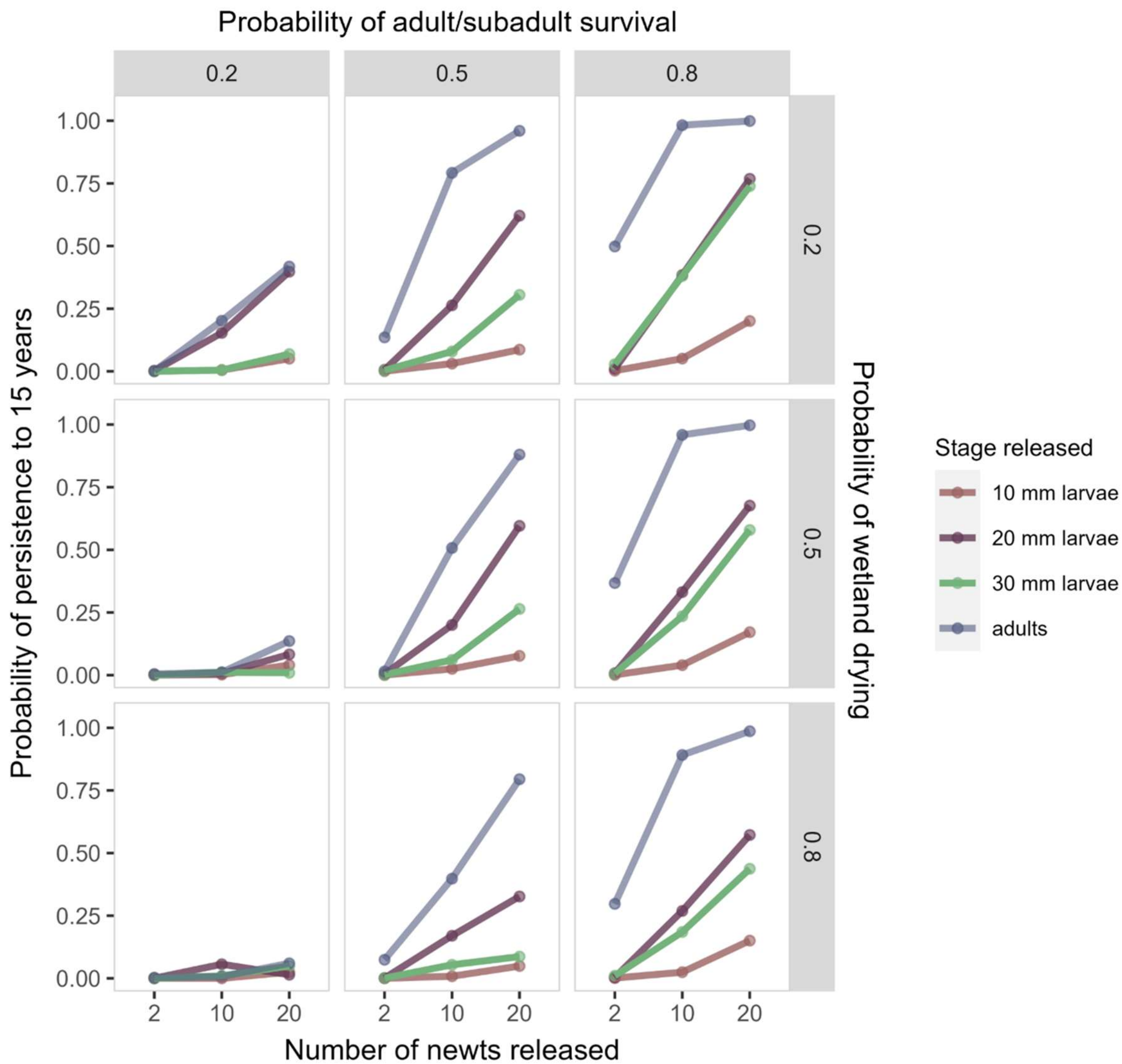

Figure 6.10. Projections of population persistence to 15 years with alternate strategies for Striped Newt repatriation and under varying demographic and environmental parameters. Each point represents a release strategy, varying by number and size or life stage of Striped Newts released. Each of the nine panels represents a different combination of values for the probability of adult/subadult survival and of wetland drying.

CHAPTER 7

NOTOPHTHALMUS PERSTRIATUS (STRIPED NEWT): TREATMENT OF CHYTRID FUNGUS IN CAPTIVITY[9]

[9]Navis, C. J., V. C. K. Terrell and J. C. Maerz. Submitted to *Herpetological Review*, September 2023.

Notophthalmus perstriatus is a state-threatened species in both states in its distribution (Georgia and Florida). Numerous entities are involved in captive propagation of the species for repatriation or as assurance colonies. To reduce the potential for spread of disease between captive and wild populations, there is a need for safe treatment of disease in captive animals. *Batrachochytrium dendrobatidis* (*Bd*) is a common fungal pathogen associated with declines of amphibian populations around the globe. To the best of our knowledge, there are no published reports of effective treatment of *Bd* in captive *N. perstriatus.*

On 20 March 2022 we collected a gravid female *N. perstriatus* from Taylor County, Georgia to hold until oviposition and supplement eggs produced by our existing captive breeding colony. The gravid female was housed alone in an indoor aquarium at our research facility in Athens, Georgia, and began laying eggs within 48 hours of collection. Oviposition occurred on the floor of the aquarium rather than on provided plants, which we interpreted as a sign of stress following collection and transport; none of the eggs developed. On 10 April 2022, that newt was found deceased in the aquarium. There were no outward physical or other behavioral signs of disease prior to death. At that time, we enacted strict biosecurity measures to limit the possibility of shared husbandry equipment spreading pathogens between aquaria; however, the first death of a newt in our existing indoor colony followed 21 days later. Following the second newt's death, the room in which newts were housed was limited to essential personnel, and husbandry was conducted solely by the lead researcher (CJN) to reduce any additional inadvertent cross-contamination. However, six additional newts in the colony died between 5 May and 23 May 2022. None displayed outward signs of illness prior to being found deceased except one adult male that was found unresponsive and unable to right himself and was euthanized. After the death of a newt, any individuals that had been co-housed with it were moved to a clean aquarium.

Several dead newts were submitted to the Southeastern Cooperative Wildlife Disease Study (SCWDS) for necropsy and pathogen testing. Some of these could not be definitively tested for pathogens due to methods of preservation. On 2 June 2022 we were notified that the final two deceased newts had tested positive for *Bd* and negative for *Batrachochytrium salamandrivorans* (*Bsal*) and *Ranavirus*. Chytridiomycosis, caused by *Bd*, was identified as the probable cause of death.

On 3 July 2022, we swabbed all remaining adult and juvenile newts housed in the colony to determine pre-treatment *Bd* infection status. Results later showed that six of the nine were positive for *Bd*, including one newt that had never been housed with an individual that died. One newt tested negative for *Bd* despite having been housed with a deceased individual. Prior to receiving the test results, all were started on a 7-day antifungal treatment. Each newt was individually housed in a bath of 1.25 µg/ml voriconazole solution, with secondary housing containers (946 mL deli cups) and treatment solution changed out daily. We selected this concentration because similar or slightly higher voriconazole concentrations were shown to have minimal negative side effects to anuran tadpoles and adult salamandrids (Martel et al. 2011, Med. Mycol. 49:143-149; Blooi et al. 2015, Sci. Rep. 5:11788). After four days of treatment, each treated newt was placed into a clean deli cup with dechlorinated water and four live blackworms and given the opportunity to feed for approximately 90 minutes before placement into the next treatment bath. Only two individuals ate a small amount during that time.

Following completion of the treatment course, all newts were retained in individual deli cups of dechlorinated water to confirm resumption of feeding; they were then returned to clean, individual aquaria. Eight of the nine newts declined in mass during treatment (mean wet mass loss = 6.85%, SE = 1.13), potentially due to fasting during that period. However, all but one had regained a portion of that mass over the 122 days post-treatment. Samples collected on 31 August 2022, 52 days post-treatment, were negative for *Bd* for all nine individuals, indicating that the voriconazole treatment regimen had successfully cleared the six infected newts and the other newts remained *Bd* negative.

To the best of our knowledge, this is the first published record of treatment of *Bd* for *N. perstriatus*. We consider this regimen to be a good option for treatment of *Bd* in captive newts due to this efficacy and minimal, short-term side effects. It is possible that the temporary body mass losses we observed might be mitigated by providing food daily or continuously through the 7-day course of treatment. Housing newts in larger secondary housing furnished with artificial plants may also reduce stress and encourage feeding during treatment. We opted to house the newts during treatment in small containers without additional enrichment for ease of care and daily sanitization. The deaths we observed occurred up to 43 days after the last opportunity for *Bd* to have been introduced into their aquaria and asymptomatic newts tested positive for *Bd* a full 12 weeks after last likely exposure. Quarantine alone therefore may not reveal *Bd* infection in all newts. In situations where strict biosecurity of captive *N. perstriatus* populations is desired, testing during quarantine may be needed to confirm that newly added animals are free of *Bd*.

All newts were collected and held for research under permits of the University of Georgia IACUC and Georgia Department of Natural Resources and were provided care consistent with the SSAR Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research; treatment for *Bd* was carried out in compliance with both permits and in communication with both permitting entities. We thank M. Yabsley of the Southeastern Cooperative Wildlife Disease Study for facilitating testing of newts, and S. Harvey of the UGA College of Veterinary Medicine for assistance procuring the antifungal for treatment.

CHAPTER 8

CONCLUSIONS

The research presented in this dissertation contributes new knowledge about the natural history of Striped Newts and methods for their conservation, but beyond that I hope that this research is exemplary of a particular *approach* to conservation. Most researchers and practitioners concerned with the conservation of rare wildlife species are not focused on Striped Newts, but many are similarly considering how to make conservation decisions for data-deficient species with poorly understood life histories and ecologies, challenged by the difficulty of obtaining additional data on rare and difficult-to-detect animals, and feeling the urgency of enacting conservation measures despite limited information with which to guide their decisions. Many are faced with similar choices to protect habitat or otherwise restrict human activity for the benefit of imperiled species—including many rarely-noticed and little-appreciated animals or plants that bear little resemblance to popular charismatic, large animal "poster children" of species conservation.

Much remains not well known about the life history and population dynamics of even my one focal Striped Newt population—let alone about ways those dynamics may differ between populations or about how those population differences might necessitate adaptation of approaches to best meet conservation objectives for local initiatives and the species overall. The ways I have approached research questions surrounding Striped Newt conservation can serve, however, as a template or jumping-off point as the field continues to build knowledge about the species and adapt practices to make progress towards conservation goals. I have not provided here one “correct” way to do conservation in a particular place, but strived to highlight the value of testing assumptions, the capacity for conducting research without needing to put practical conservation efforts on hold, and the importance of examining the socio-ecological context and history of the places where conservation work is being done as a vital component of making just and effective conservation and land management decisions.

Framing the research questions

From the beginning, my work on Striped Newts has been centered around relevance to conservation practice—which is also a core criteria for research in the Integrative Conservation (ICON) PhD program (ICON 2023). Through conversations with my advisor during my first semester, I settled on Striped Newts as a regional species of high conservation priority but with many remaining gaps in knowledge—however, I had yet to define the exact direction of my dissertation research. That winter, I first attended a meeting of the Striped Newt Working Group (SNWG), a somewhat informally organized network of researchers, conservation practitioners, land managers, government agency representatives, and others concerned with conservation of the species. It was through hearing updates about ongoing and planned conservation efforts that I began to formulate the particulars of my research plans. Namely, it became clear to me that captive rearing and release of newts to re-establish or augment populations in particular locations was an important focus of conservation efforts, yet such efforts had so far resulted in minimal verified progress towards conservation goals. With several years ahead of me in which to devote my time to focusing research on questions that might help improve conservation outcomes, I set out to evaluate potential reasons that released captive-reared Striped Newts were not readily establishing and growing breeding populations at repatriation sites (Chapters 4, 5).

The Striped Newt population at Sandhills WMA (SWMA) had not yet been the subject of in-depth research, and state managers had interest in estimation of the population and characterization of its ecological responses. Another need identified by professionals involved in Striped Newt conservation work was development of a working population model, which became another objective of my research. While detection challenges revealed during my years-long field study at SWMA (Chapter 3) prevented me from completing some of my population estimation objectives, data from that field research were valuable to defining the structure of and parameterizing the Striped Newt population viability model presented in Chapter 6. Those population insights also helped illuminate potential misconceptions about wild Striped Newt life history and population dynamics (specifically, the existence of important differences between populations or distinct population segments that invalidate assumptions of consistent ecological responses, species-wide) that exacerbate mismatches between captive rearing practices and repatriation objectives.

Transdisciplinary collaboration and knowledge production

This applied focus of my research meant that it was necessarily transdisciplinary, crossing academic/non-academic boundaries to engage and collaborate with practitioners outside of academia (King and Nibbelink 2019). Contacts at nongovernmental organizations (NGOs) involved in Striped Newt conservation provided valuable advice and insights as I planned for the captive breeding colony used in my research, and the captive rearing practices I employed were closely based on those used by zoos and other NGOs already engaging in Striped Newt captive breeding (Means et al. 2014, 2015, Mendyk and Beshel 2017) so that my results would be most relevant to that work. Likewise, as additional organizations and individuals became involved with Striped Newt conservation work over the years of my PhD, I regularly shared from my own knowledge and experiences to assist them in getting started with their own captive breeding and research work.

This was an area where it was important to be aware of my own positionality—reflexivity, defined in this context as involving "critical reflection on one's own positionality and the power relations involved in environmental knowledge production" (ICON 2023), is a core practice ICON students employ while developing and conducting dissertation research. I am (among other things) a PhD student; someone with a background of access to research experiences that had shaped my knowledge base and perspectives on wildlife conservation and research; a white woman; and someone connected to a research lab with an existing network of connections that helped me get established in my own research work. At the same time, I entered the Striped Newt conservation scene as someone new to the U.S. Southeast and to working on this species; there are researchers and practitioners in the region who have been involved in Striped Newt conservation in some capacity for years to decades. At times, practitioners who were still newer to Striped Newt conservation work or who had less of a formal research background expressed deference to me as a PhD student or hesitance about their own limited experience or advanced degrees. It was important to me to expressly counter notions that someone pursuing a certain degree or with more present experience working on the species was necessarily more capable of valuable insights and contributions to the ongoing development of Striped Newt conservation strategies, and to encourage those practitioners to engage and contribute their own unique perspectives and ideas. While being a PhD student allowed me the opportunity to devote a great deal of time to research over several years, of course academic research is not the only manner in which knowledge about species or conservation practices is produced.

Indeed, I have observed both benefits and challenges of the various ways that knowledge about Striped Newts and related conservation strategies is often produced and shared. Insights about Striped Newt conservation practice and research are often shared informally. There has been relatively limited research about the species published in scientific journals (and such journals may not be easily accessible to practitioners outside of academic institutions), and informal or personal knowledge is frequently shared through direct interpersonal interactions. Forums that facilitate such interaction, such as SNWG meetings and other regional conferences, can provide excellent opportunities for such communication and reciprocal knowledge sharing. Without established connections to those settings and individuals, however, it can be a challenge for those seeking to become involved in Striped Newt conservation work to gain access to the unpublished or personal knowledge needed to develop their own effective conservation approaches and avoid replicating the same trial-and-error processes.

Such personal knowledge—whether gained through field research or conservation work, involvement in captive husbandry, familiarity with habitat management practices, or other experiences—is not necessarily less “correct” than conclusions drawn from published research. However, besides the limits to broad access to such knowledge, reliance on informal knowledge-sharing can risk reinforcement of untested or misinterpreted concepts. This is something that I, too, have fallen into—accepting knowledge about Striped Newt life history and ecology that is commonly repeated (including in publication, or based upon published research) without closely examining the bases of those ideas. This is an understandable inclination: when limited data exist, conservation decisions must nonetheless be made based on that incomplete information, extrapolating from and generalizing what has been previously established in limited contexts. I even intentionally employed a similar approach when parameterizing my population viability model (Chapter 6). If that knowledge goes unexamined and untested as it is applied to novel situations, however, there is a risk of continually devoting time and resources to conservation approaches that do not result in the desired or anticipated outcomes. One of the challenges of this research has been to find a balance between recognizing the valuable insights that can come from less formal forms of knowledge production—gained from personal experiences or sparked by anecdotal observations—while at the same time seeking to demonstrate the value of testing assumptions, intentionally seeking to build upon and revise knowledge, and continually adapting conservation approaches if decisions based on existing notions are not bringing about the desired results.

My desire to conduct research that was applicable and useful to conservation practice guided not only the development of my research questions and the ways I engaged with and learned from non-academic practitioners, but my approaches to crafting the products of that research. For instance, when writing code and documentation for my population model (Chapter 6) I aimed for ease of use by researchers and decision-makers who may not have deep familiarity with R code. I structured the code so that someone wishing to compare alternate scenarios or update parameter values based on the latest Striped Newt data can input values into clear documents, in more familiar formats, that are read into the model. I also did not want the code itself to be an indecipherable "black box" to all but those with high levels of R proficiency, and so annotated the model code with the aim of making clear the functions and assumptions of various steps.

I also considered it important to share in this dissertation not only the "successful" components of my research—i.e., those that produced clear results on which conclusions might be justifiably based—but also the obstacles I encountered that hindered me in full completion of my research aims (e.g., Chapter 3), pilot projects that decidedly did not go as anticipated (Chapter 5), and outcomes of unintended disease introduction during captive husbandry of my newts (Chapter 7). I hope that sharing those lessons learned will be useful in allowing other researchers and practitioners to advance the development of their own work, rather than replicating the same errors or running into the same unanticipated challenges. I hope also that sharing those portions of my work will contribute to a model of openness to learning and adapting approaches to conservation challenges, humility about one's own knowledge and expertise, and transparency about both successes and failures for the purpose of furthering the collective progress that can be made by conservation communities towards shared objectives.

Challenges of integrative research

Engaging in integrative research is generally a more daunting undertaking than limiting one's research focus to traditional approaches within academic, disciplinary silos. It requires devoting a great deal of time and energy to engaging with other disciplines and epistemological perspectives, considering the complex nature of any conservation issue not only when developing research questions but in the practice of conducting the research to answer them. I considered it important to understand—and highlight the value of understanding—the social and ecological contexts of the area in which I was conducting field research, rather than simply viewing it in isolation as the site of a Striped Newt population for me to study. Critical scholarship considering "fortress" models of conservation or the sustainability of traditional lifeways often focus on portions of the Global South that have undergone relatively limited development and where more "wilderness" remains. In the southeastern U.S., land use changes and shifting power dynamics of who maintains governance over and access to natural resources are to a degree historical realities rather than pressing ongoing concerns. However, conservation work on these landscapes is deserving of similarly nuanced scrutiny through multiple lenses. While the United States as a whole includes a relatively large proportion of public land (protected to varying degrees), the majority is in western states. Meanwhile, the Southeast is home to high levels of biodiversity and concentrations of endemic species (Jenkins et al. 2015). Prioritizing changes to land use for species conservation—whether through conservation easements on private lands or conversion of privately owned properties to public lands that limit human activities—means there is a need to wrestle with questions of how land management decisions interact with human use of, access to, and enjoyment of those landscapes and how those decisions might alleviate or entrench existing power dynamics.

Historical ecological studies by necessity involve bridging social and natural science approaches to illuminate a more complete (though never perfect) picture of the ways human societies and the rest of ecosystems have interacted and shaped one another over time (Szabó 2015). While not every practice resulted in relevant insights that ended up incorporated into Chapter 2, examining that context required me to use methods that are not common in most ecological research, including use of archival materials to provide insights on interacting social and environmental histories across multiple scales (Szabó 2015, Guldi 2016); analysis of historical maps and aerial photographs to understand land-use changes, trace human population patterns, and tie historical accounts to present-day known locations (Santana-Cordero and Szabó 2019); and utilization of a wide variety of sources of information—such as public records, scans of historical newspapers and newsletters, personal journals, advertisements, letters, rail system records, and photographs (Jordanova 2016)—that are not regularly considered reliable sources of knowledge in traditional natural science research. Indeed, much of my approach to the historical research that became Chapter 2 required a source critical approach to historical accounts describing ecological or sociopolitical circumstances, understanding that individual authors' accounts did not represent a complete and objective "truth" but reflected the positionality of their creators and the power dynamics and social forces at play in the author's place and time (Santana Cordero et al. 2014, Coello de la Rosa and Dieste 2020). I had to consider which voices and perspectives were well-represented in historical documents and accounts, and which were largely excluded due to prejudicial power dynamics or because groups historically prioritized other forms of knowledge transmission (i.e., other than written accounts). Written accounts of the earliest peoples of the region are absent prior to colonization, with later accounts largely crafted by outside observers as white settlers and explorers began writing about the peoples they encountered. The experiences of enslaved Black residents are likewise poorly documented, particularly as expressed from their own perspectives. Some oral histories provided by formerly enslaved Black residents of southwestern Georgia were documented early in the twentieth century, but broadly speaking the perspectives and experiences of marginalized groups within societies remain underrepresented and undervalued to this day. Such exclusion of less-privileged perspectives can manifest on multiple scales. For instance, I was strongly interested in tracing the particulars of land ownership and use for the area that today makes up the eastern tract of SWMA, from the time such personal property ownership began. I began by identifying the corresponding land parcels distributed in 1827 land lottery, and combing through the land lottery records for the names of the "fortunate drawers" granted the opportunity to own those plots. While the land lotteries were primarily open only to white men—not a group generally underrepresented from the historical record—they also allowed for participation of the widows or orphans of men who would have been eligible. Incidentally, the majority of land lots corresponding to present-day SWMA were assigned to such widow or orphan lottery participants. Those individuals' own names were not recorded in the land lottery records, making it difficult to trace the ongoing activities of those individuals and uses of their properties by locating additional public records or other archival materials linked to their names.

Oral histories can be particularly valuable towards understanding more recent changes in local ecosystems and the role that humans played in shaping (and being shaped by) them (Santana Cordero et al. 2014), and my original plan was to incorporate more personal insights into the narrative of Chapter 2. I had hoped to conduct additional semi-structured interviews with a variety of stakeholders to the land that makes up SWMA, including hunters, other recreational users, surrounding land owners, and other community members as well as agency officials or researchers involved in the present-day land management and species conservation functions of the property. However, making contact and connection with such parties in sparsely-populated rural areas (particularly where a researcher does not live and have existing community connections) is often eased via introductions through existing contacts. I ran into barriers of not receiving a response from some potential interviewees I contacted—including some who may have been quite helpful in identifying and facilitating connection to a broader range of area stakeholders—and others suggesting interviewees I'd already contacted.

It might have been possible to seek out other ways of introducing myself and my research goals to community members by spending additional time in the area and working to identify community gathering places that might be a venue for making such introduction and inviting participation. However, the onset of the COVID-19 pandemic not long after I began my field work brought on an opposing suite of considerations. I was traveling, along with limited accompaniment of colleagues who assisted me with field work during the height of the pandemic, from a university town with numerous healthcare facilities and with COVID testing more readily accessible through the university than it was for many Georgia residents; once vaccines became available the following year, we soon had multiple local options for accessing them. In contrast, Taylor County—and many of the other rural areas through which we traveled to reach SWMA—has limited healthcare infrastructure and relatively high rates of poverty. I felt strongly that we should not risk inadvertently introducing COVID infection to area residents, both because of the inherent risks of the virus and the additional socioeconomic risk factors involved in facing a potentially serious disease in an under-resourced rural area. I prioritized *not* coming into direct contact with community members, planning research travel to avoid the need for any stops where we might come into contact with area residents or other travelers until after vaccines were more widely available and transmission in the state had notably declined from peak rates.

Strategic communication

One of the ways I sought to regularly engage with and provide experiences to community members outside of academia was through encouraging diverse groups and individuals to join me in the field as I conducted my population and repatriation research at SWMA. In addition to undergraduates and graduate students (from my home department and others), individuals from a range of backgrounds participated in my field work and had the opportunity for direct encounters with not only Striped Newts but their habitat and the other species found in that landscape. This included early-career land management technicians working for the Georgia Department of Natural Resources; participants in the Amphibian Foundation's Bridge program, which aims to provide practical herpetology experience to students before, during, or recently graduated from college; staff of NGOs focused on conservation and research; and participants of an Athens-area community science volunteer group.

I also focused on regularly communicating with practitioners and fellow researchers involved in Striped Newt conservation work, of course. Following my first attendance at a SNWG meeting during the first year of my PhD, I presented updates on my ongoing research and its results during subsequent meetings (as well as at other regional and national/international conferences, such as Southeast Partners in Amphibian and Reptile Conservation meetings and the Joint Meeting of Ichthyologists and Herpetologists). As participants were not homogenous in educational or research backgrounds, experiences with various components of Striped Newt conservation work (e.g., field research or monitoring vs. captive breeding), or current work settings, sometimes it was necessary to establish a background of shared concepts. One challenge of estimating the population outcomes of Striped Newt repatriation efforts was that common captive rearing protocols frequently result in a developmental route not known to occur in Striped Newts in the wild; with no easy "stage" category to assign them, frequently such individuals have been described as small adults (independent of the presence of secondary sexual characteristics) or assumed to be in transition into the terrestrial eft stage. When I presented my population viability model (chapter 6) during a meeting of the Striped Newt Working Group, it was necessary to establish a background assumption important to interpretation of my projections: that secondary sexual traits are reliably indicative of a Striped Newt's internal reproductive maturity. I referenced prior research that had confirmed that relationship, but no overly-technical scientific jargon was needed to introduce the concept. Instead, I encapsulated the principle in a brief humorous couplet, and went on to share others I had brainstormed as I prepared for the meeting (Table 8.1). A meeting participant shared their own quip created in response, and later another participant asked me for the rhyme used in my presentation so they could write it down, saying that they wanted to send it to someone else they knew and that "I'll use that forever!"

My strategic communication efforts extended beyond those directly involved in Striped Newt conservation. Georgia is incredibly rich in herpetofaunal diversity, yet it is common to encounter lifelong residents of the state who don't realize that they live in such a unique area of amphibian and reptile biodiversity. Many also carry fear or misinformation regarding snakes in particular, as several venomous species are found in the state. My aim in conducting herpetology outreach is always to meet people where they are: I never push someone to hold an animal, touch it, or even come closer to it, let alone come away liking the species or category of animal. While I took part in some outreach events where participants had chosen to attend because of an interest in herpetofauna (e.g., an open house event at the Amphibian Foundation or Snake Day at Sandy Creek Nature Center), most of my outreach was to audiences who held a spectrum of perspectives on such wildlife.

I also sought opportunities to communicate about ecology and the role of ecologists and wildlife researchers, more broadly. I may be in the minority of those involved in wildlife research and conservation, in that my story does not begin with me always out catching frogs as a child. While I have always loved animals, I grew up in a city, and did not have the same types of experiences with the outdoors that many professionals cite as the start of their passion for the field. Not everyone has regular opportunity to visit minimally-developed outdoor areas or have personal encounters with many forms of wildlife, and I have particular interest in expanding access to such knowledge and experiences by reaching out to groups that may have no prior positive experiences with wildlife or less-developed places. Descriptions of representative general-audiences communication venues are summarized below.

- Herpetology-focused events:
    - Reptile and Amphibian Open House at the Amphibian Foundation (2018)
    - Snake Day, Sandy Creek Nature Center (2022, 2023)
    - Scary Oozy Slimy Day, Sandy Creek Nature Center (2023)
    - Day on the Lawn, Warnell School of Forestry and Natural Resources (Annual)
- Community outreach events:
    - After-School Program at East Athens Community Center (2018): I and fellow graduate students introduced grade school children to reptiles and amphibians, adapting our approach to various age groups circulating among presenters.
    - STEMzone (2018, 2019): This graduate student organized science outreach event was held on the University of Georgia campus, affording opportunity to engage fans who had arrived on campus before the start of a home football game. I organized a booth in 2018 and participated in hosting it the following year, encouraging both direct encounters with outreach animals and—for those who were not comfortable interacting with reptiles and amphibians—opportunities to share knowledge, answer questions, and potentially dispel fears or myths.
    - Extra Special People (2019): I was accompanied by an undergraduate student to conduct an event where we facilitated opportunities for children and adults with disabilities to interact with reptile and amphibian animal ambassadors.

    - Barnett Shoals Elementary School (2019): A colleague and I shared information about native Georgia herpetofauna with elementary students and allowed them to make personal connections with several of the lab’s outreach animals.
    - Ag Day at East Jackson Elementary School (2022): A fellow graduate student and I presented to various ages of students as classes rotated through stations of the school’s Ag Day events, providing opportunity for interaction with reptile and amphibian outreach animals, sharing information, and answering questions.
- General outreach about being an ecologist/scientist:
    - Science Project mentor, Beaumont Middle School (2018): A middle school science teacher with whom I’d connected via social media put out a request for virtual mentors for his students completing individual science projects over several months. I corresponded with several students via email at certain stages of the process, sharing feedback and encouragement as they developed their ideas and worked through their projects.
    - Speaker Series, Gwinnett School of Mathematics Science and Technology (2019): A fellow graduate student and I presented our own journeys and experiences in becoming ecologists, to a group of high school students learning about a variety of career fields and pathways.

- Skype a Scientist (2019, 2020, 2021): I presented virtually to various grade-level classrooms, sharing my experiences as an ecologist and wildlife researcher and answering student questions about my work.
- General Ecology and Marine Biology 101 panel, Ocean Institute (2021): I joined other graduate students and professionals for a live virtual panel to share experiences and answer questions about becoming and working as an ecologist.

Table 8.1. Informal couplets used to establish shared terminology and background assumptions about Striped Newt life history. Provided are the primary version included in a presentation slide, alternatives shared during the same talk, and an option subsequently contributed by a meeting attendee.

Primary	If the cloaca's not hearty, it's not down to party!
Alternative	If the cloaca's not swole, it's not ready to roll!
	Larvae lost gills—life stages shaky? You've gotta check for those swollen cloacae!
Contributed	If the cloaca's not plump, it's not ready to hump!

REFERENCES

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

Akkoç, C. C., and L. E. Williams. 2005. Population modeling for a captive squirrel monkey colony. American Journal of Primatology 65:239–254.

Ambinakudige, S., D. Parisi, and S. M. Grice. 2012. An analysis of differential migration patterns in the Black Belt and the New South. Southeastern Geographer 52:146–163.

Araki, H., B. Cooper, and M. S. Blouin. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318:100–103.

Armstrong, C. 2017. Frederick Law Olmsted and the cultural geography of southern slave autonomy. Slavery & Abolition 38:37–48.

Armstrong, C. G., and J. R. Veteto. 2015. Historical ecology and ethnobiology: Applied research for environmental conservation and social justice. Ethnobiology Letters 6:5.

Ayers, E. L. 2007. The Promise of the New South: Life After Reconstruction. 15th Anniversary Edition. Oxford University Press, New York, NY.

Bailey, L. L., and J. D. Nichols. 2009. Capture-mark-recapture, removal sampling, and occupancy models. Pages 447–463 *in* C. K. Dodd, editor. Amphibian Ecology and Conservation: A Handbook of Techniques. Oxford University Press, New York, NY.

Balée, W. 2006. The research program of historical ecology. Annual Review of Anthropology 35:75–98.

Balée, W. L. 1998. Advances in Historical Ecology. Columbia University Press, New York, NY.

Barrajón, E., and L. Barrajón. 2020, December 15. Effect of right censoring bias on survival analysis. arXiv 2012.08649v1.

Barri, F. R. 2016. Reintroducing guanaco in the upper belt of central Argentina: Using population viability analysis to evaluate extinction risk and management priorities. PLOS ONE 11:e0164806.

Bartram, W. 1791. Travels through North and South Carolina, Georgia, East and West Florida. James and Johnson, Philadelphia, PA.

Becher, D. 2023. Land inequalities in the United States. Annual Review of Sociology 49:421–441.

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

Berkowic, D., and S. Markman. 2019. Weighing density and kinship: Aggressive behavior and time allocation in fire salamander (*Salamandra infraimmaculata*). PLOS ONE 14:e0220499.

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

Biersack, A. 2006. Reimagining political ecology: Culture/power/history/nature. Pages 3–42 *in* A. Biersack and J. B. Greenberg, editors. Reimagining Political Ecology. Duke University Press, Durham, NC.

Bishop, S. C. 1941. Notes on salamanders with descriptions of several new forms. Occasional Papers of the Museum of Zoology, University of Michigan 451:1–21.

Bizzari, L. E., C. D. Collins, L. A. Brudvig, and E. I. Damschen. 2015. Historical agriculture and contemporary fire frequency alter soil properties in longleaf pine woodlands. Forest Ecology and Management 349:45–54.

Black, J. H. 1976. Environmental fluctuations in central Oklahoma temporary ponds. Proceedings of the Oklahoma Academy of Science 56:1–8.

Blaustein, A. R., and L. K. Belden. 2003. Amphibian defenses against ultraviolet-B radiation. Evolution & Development 5:89–97.

Blaustein, A. R., J. M. Kiesecker, D. P. Chivers, D. G. Hokit, A. Marco, L. K. Belden, and A. Hatch. 1998. Effects of ultraviolet radiation on amphibians: Field experiments. American Zoologist 38:799–812.

Bloxam, Q. M. C., and S. J. Tonge. 1995. Amphibians: Suitable candidates for breeding-release programmes. Biodiversity & Conservation 4:636–644.

Blum, E. D. 2002. Power, danger, and control: Slave women's perceptions of wilderness in the nineteenth century. Women's Studies 31:247–265.

Bodinof, C. M., J. T. Briggler, R. E. Junge, J. Beringer, M. D. Wanner, C. D. Schuette, J. Ettling, R. A. Gitzen, and J. J. Millspaugh. 2012. Postrelease movements of captive-reared Ozark Hellbenders (*Cryptobranchus alleganiensis bishopi*). Herpetologica 68:160–173.

Bohenek, J. R., and W. J. Resetarits. 2018. Are direct density cues, not resource competition, driving life history trajectories in a polyphenic salamander? Evolutionary Ecology 32:335–357.

Boveng, P. L., J. M. V. Hoef, D. E. Withrow, and J. M. London. 2018. A Bayesian analysis of abundance, trend, and population viability for harbor seals in Iliamna Lake, Alaska. Risk Analysis 38:1988–2009.

Bowkett, A. E. 2009. Recent captive-breeding proposals and the return of the ark concept to global species conservation. Conservation Biology 23:773–776.

Bradke, D. R., B. A. Crawford, M. Kaylor, and J. C. Maerz. 2024. Evaluating uncertainty to improve a common monitoring method and guide management decisions for diamond-backed terrapins. The Journal of Wildlife Management 88:e22513.

Brand, L. R., M. Hussey, and J. Taylor. 2003. Decay and disarticulation of small vertebrates in controlled experiments. Journal of Taphonomy 1:69–95.

Brehm, J. M., B. W. Eisenhauer, and R. C. Stedman. 2013. Environmental concern: Examining the role of place meaning and place attachment. Society and Natural Resources 26:522–238.

Brodie, E. D. 1968. Investigations on the skin toxin of the red-spotted newt, *Notophthalmus viridescens viridescens*. The American Midland Naturalist 80:276–280.

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

Brudvig, L. A., E. Grman, C. W. Habeck, J. L. Orrock, and J. A. Ledvina. 2013. Strong legacy of agricultural land use on soils and understory plant communities in longleaf pine woodlands. Forest Ecology and Management 310:944–955.

Brudvig, L. A., N. E. Turley, S. L. Bartel, L. Bell-Dereske, S. Breland, E. I. Damschen, S. E. Evans, J. Gibbs, P. G. Hahn, R. Isaacs, J. A. Ledvina, J. L. Orrock, Q. M. Sorenson, and J. D. Stuhler. 2021. Large ecosystem-scale effects of restoration fail to mitigate impacts of land-use legacies in longleaf pine savannas. Proceedings of the National Academy of Sciences 118:e2020935118.

Bucciarelli, G. M., M. A. Clark, K. S. Delaney, S. P. D. Riley, H. B. Shaffer, R. N. Fisher, R. L. Honeycutt, and L. B. Kats. 2020. Amphibian responses in the aftermath of extreme climate events. Scientific Reports 10:3409.

Bürgi, M., and E. W. B. Russell. 2001. Integrative methods to study landscape changes. Land Use Policy 18:9–16.

Burlacu, L., C. Radu, T. Sahlean, and I.-C. Gavriloaie. 2009. Inter and intra specific cannibalism and aggressiveness within the *Triturus cristatus* superspecies: hungry or crowded? Aquaculture, Aquarium, Conservation & Legislation 2:161–183.

Burrow, A. K., B. A. Crawford, and J. C. Maerz. 2021. Ground cover and native ant predation influence survival of metamorphic amphibians in a southeastern pine savanna undergoing restoration. Restoration Ecology 29:e13410.

Burton, J. L., E. Robinson, and S. Ye. 2012. Spatially explicit agent-based model of striped newt metapopulation dynamics under precipitation and forest cover scenarios. Pages 63–83 *in* J. D. Westervelt and G. L. Cohen, editors. Ecologist-Developed Spatially-Explicit Dynamic Landscape Models. Springer US, Boston, MA.

Cable, J. 2013. The roots of organized resistance: African American political mobilization in southwest Georgia, 1918-1945. The Corinthian 14:Article 4.

Campbell, J. F. 2004. Textualising slavery: From "slave" to "enslaved people" in Caribbean historiography. Pages 34–45 *in* S. Courtman, editor. Beyond the Blood, the Beach & the Banana: New Perspectives in Caribbean Studies. Ian Randle Publishers, Kingston, Jamaica.

Canessa, S., P. Genta, R. Jesu, L. Lamagni, F. Oneto, S. Salvidio, and D. Ottonello. 2016. Challenges of monitoring reintroduction outcomes: Insights from the conservation breeding program of an endangered turtle in Italy. Biological Conservation 204:128–133.

Canessa, S., D. Hunter, M. McFadden, G. Marantelli, and M. A. McCarthy. 2014. Optimal release strategies for cost-effective reintroductions. Journal of Applied Ecology 51:1107–1115.

Canessa, S., D. Ottonello, G. Rosa, S. Salvidio, E. Grasselli, and F. Oneto. 2019. Adaptive management of species recovery programs: A real-world application for an endangered amphibian. Biological Conservation 236:202–210.

Carey, A. G. 2011. Sold Down the River: Slavery in the Lower Chattahoochee Valley of Alabama and Georgia. University of Alabama Press, Tuscaloosa, AL.

Carey, C., and M. A. Alexander. 2003. Climate change and amphibian declines: is there a link? Diversity and Distributions 9:111–121.

Carter, P. A. 1997. Maintenance of the Adh polymorphism in *Ambystoma tigrinum nebulosum* (tiger salamanders). I. Genotypic differences in time to metamorphosis in extreme oxygen environments. Heredity 78:101–109.

Cathey, R. A. 1972. Forest Statistics for Central Georgia, 1972. Forest Service, U.S. Department of Agriculture, Southeastern Forest Experiment Station, Asheville, NC.

Cayot, L. J. 2020. Española Island: From near extinction to recovery. Pages 435–450 *in* J. P. Gibbs, L. J. Cayot, and W. T. Aguilera, editors. Galapagos Giant Tortoises. Academic Press, London, UK.

Cayuela, H., A. C. R. Lackey, V. Ronget, B. Monod-Broca, and H. H. Whiteman. 2024. Polyphenism predicts actuarial senescence and lifespan in tiger salamanders. Journal of Animal Ecology 93:333–347.

Chandler, H. C., A. L. Rypel, Y. Jiao, C. A. Haas, and T. A. Gorman. 2016. Hindcasting historical breeding conditions for an endangered salamander in ephemeral wetlands of the southeastern USA: Implications of climate change. PLOS ONE 11:e0150169.

Choy, D. L., J. Wadsworth, and D. Burns. 2010. Seeing the landscape through new eyes: Identifying and incorporating indigenous landscape values into regional planning processes. Australian Planner 47:178–190.

Christensen, E. M., A. J. Lawson, E. Rivenbark, P. K. London, D. Castellanos, J. C. Culbertson, S. M. DeMay, C. Eakin, L. S. Pearson, K. Soileau, H. Waddle, and C. P. McGowan. 2024. Accounting for multiple uncertainties in a decision-support population viability assessment. Biological Conservation 299:110811.

Coello de la Rosa, A., and J. L. M. Dieste. 2020. In Praise of Historical Anthropology: Perspectives, Methods, and Applications to the Study of Power and Colonialism. Routledge, New York, NY.

Comizzoli, P., and W. V. Holt. 2019. Breakthroughs and new horizons in reproductive biology of rare and endangered animal species. Biology of Reproduction 101:514–525.

Conde, D. A., J. Staerk, F. Colchero, R. Da Silva, J. Schöley, H. M. Baden, L. Jouvet, J. E. Fa, H. Syed, E. Jongejans, S. Meiri, J.-M. Gaillard, S. Chamberlain, J. Wilcken, O. R. Jones, J. P. Dahlgren, U. K. Steiner, L. M. Bland, I. Gomez-Mestre, J.-D. Lebreton, J. González Vargas, N. Flesness, V. Canudas-Romo, R. Salguero-Gómez, O. Byers, T. B. Berg, A. Scheuerlein, S. Devillard, D. S. Schigel, O. A. Ryder, H. P. Possingham, A. Baudisch, and J. W. Vaupel. 2019. Data gaps and opportunities for comparative and conservation biology. Proceedings of the National Academy of Sciences 116:9658–9664.

Conroy, M. J., and J. P. Carroll. 2009. Using Models in Conservation Biology. John Wiley & Sons, Ltd, Chichester, West Sussex, UK.

Cordero-Rivera, A., and R. Stoks. 2008. Mark–recapture studies and demography. Pages 7–20 *in* A. Córdoba-Aguilar, editor. Dragonflies and Damselflies. First Edition. Oxford University Press, Oxford, UK.

Cotterill, R. S. 1917. The telegraph in the South, 1845-1850. South Atlantic Quarterly 16:149–154.

Coughlan, M. R., and D. R. Nelson. 2018. Influences of Native American land use on the Colonial Euro-American settlement of the South Carolina Piedmont. PLOS ONE 13:e0195036.

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

Crane, A., and A. Mathis. 2015. Observation of predation by a lycosid spider on a captive-reared salamander larva (*Ambystoma annulatum*). Herpetology Notes 8:455–457.

Crates, R., D. Stojanovic, and R. Heinsohn. 2023. The phenotypic costs of captivity. Biological Reviews 98:434–449.

Crawford, B. A., J. C. Maerz, V. C. K. Terrell, and C. T. Moore. 2022. Population viability analysis for a pond-breeding amphibian under future drought scenarios in the southeastern United States. Global Ecology and Conservation 36:e02119.

Cronin, J. T., and J. Travis. 1986. Size-limited predation on larval *Rana areolata* (Anura: Ranidae) by two species of backswimmer (Insecta: Hemiptera: Notonectidae). Herpetologica 42:171–174.

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

Cushman, E. 2011. The Cherokee syllabary: A writing system in its own right. Written Communication 28:255–281.

Daly, G., P. Johnson, G. Malolakis, A. Hyatt, and R. Pietsch. 2011. Reintroduction of the Green and Golden Bell Frog *Litoria aurea* to Pambula on the south coast of New South Wales. Australian Zoologist 34:261–270.

Daniszewski, J. 2020. The decision to capitalize Black. https://blog.ap.org/announcements/the-decision-to-capitalize-black.

Davis, C. L., D. A. W. Miller, S. C. Walls, W. J. Barichivich, J. Riley, and M. E. Brown. 2017. Life history plasticity does not confer resilience to environmental change in the mole salamander (*Ambystoma talpoideum*). Oecologia 183:739–749.

Dehghan, M. H., and T. Duchesne. 2011. A generalization of Turnbull's estimator for nonparametric estimation of the conditional survival function with interval-censored data. Lifetime Data Analysis 17:234–255.

Della Togna, G., L. G. Howell, J. Clulow, C. J. Langhorne, R. Marcec-Greaves, and N. E. Calatayud. 2020. Evaluating amphibian biobanking and reproduction for captive breeding programs according to the Amphibian Conservation Action Plan objectives. Theriogenology 150:412–431.

Denoël, M., F. Hervant, R. Schabetsberger, and P. Joly. 2002. Short- and long-term advantages of an alternative ontogenetic pathway. Biological Journal of the Linnean Society 77:105–112.

Denoël, M., A. Ivanović, G. Džukić, and M. L. Kalezić. 2009. Sexual size dimorphism in the evolutionary context of facultative paedomorphosis: Insights from European newts. BMC Evolutionary Biology 9:278.

Denoël, M., and P. Joly. 2000. Neoteny and progenesis as two heterochronic processes involved in paedomorphosis in *Triturus alpestris* (Amphibia: Caudata). Proceedings of the Royal Society of London. Series B: Biological Sciences 267:1481–1485.

Denoël, M., P. Joly, and H. H. Whiteman. 2005. Evolutionary ecology of facultative paedomorphosis in newts and salamanders. Biological Reviews 80:663–671.

Denver, R. J. 1997. Proximate mechanisms of phenotypic plasticity in amphibian metamorphosis. American Zoologist 37:172–184.

DeVore, J. L. 2011. An exercise in complexity: Indirect influences of invasion by an exotic grass (*Microstegium vimineum*) on forest floor food webs. University of Georgia, Athens, GA.

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

Dodd, C. K. 1996. Use of terrestrial habitats by amphibians in the sandhill uplands of north-central Florida. Alytes 14:42–52.

Dodd, C. K. J., and B. S. Cade. 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. Conservation Biology 12:331–339.

Dodd, C. K. J., D. B. Means, and S. A. Johnson. 2005. *Notopthalmus perstriatus*. Page 887 *in* M. Lannoo, editor. Amphibian Declines: The Conservation Status of United States Species. University of California Press, Berkeley, CA.

Dodd, C. K., and S. A. Johnson. 2007. Breeding ponds colonized by Striped Newts after 10 or more years. Herpetological Review 38:150–152.

Dodd, C. K., and L. V. LaClaire. 1995. Biogeography and status of the striped newt (*Notophthalmus perstriatus*) in Georgia, USA. Herpetological Natural History 3:37–46.

Dodd, C. K., and R. A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: Are they conservation strategies that work? Herpetologica 47:336–350.

Doster, J. F. 1964. The Georgia Railroad & Banking Company in the Reconstruction era. The Georgia Historical Quarterly 48:1–32.

Ducey, P. K., and J. Dulkiewicz. 1994. Ontogenetic variation in antipredator behavior of the newt *Notophthalmus viridescens*: Comparisons of terrestrial adults and efts in field and laboratory tests. Journal of Herpetology 28:530–533.

EBCI. 2024. Government – Eastern Band of Cherokee. https://ebci.com/government/.

Edwards, S. C. 2001. "To do the manufacturing for the South": Private industry in Confederate Columbus. The Georgia Historical Quarterly 85:538–554.

Enge, K. M., A. L. Farmer, J. D. Mays, T. D. Castellon, E. P. Hill, and P. E. Moler. 2014. Survey of Winter-Breeding Amphibian Species. Florida Fish and Wildlife Conservation Commission, Gainesville, FL.

Farmer, A. L., K. M. Enge, J. B. Jensen, D. J. Stevenson, and L. L. Smith. 2017. A range-wide assessment of the status and distribution of the Striped Newt (*Notophthalmus perstriatus*). Herpetological Conservation and Biology 12:585–598.

Faust, L. J., S. D. Thompson, J. M. Earnhardt, E. Brown, S. Ryan, M. Sherman, and M. Yurenka. 2003. Using stage-based system dynamics modeling for demographic management of captive populations. Zoo Biology 22:45–64.

Finlay, M. R. 1997. The failure of chemurgy in the depression-era South: The case of Jesse F. Jackson and the Central of Georgia Railroad. The Georgia Historical Quarterly 81:78–102.

Finney, C. 2014. Black Faces, White Spaces: Reimagining the Relationship of African Americans to the Great Outdoors. First edition. University of North Carolina Press, Chapel Hill, NC.

Fisher, M. C., F. Pasmans, and A. Martel. 2021. Virulence and pathogenicity of chytrid fungi causing amphibian extinctions. Annual Review of Microbiology 75:673–693.

Florida Fish and Wildlife Conservation Commission. 2022. Species conservation measures and permitting guidelines: Striped newt *Notophthalmus perstriatus*. Florida Administrative Register.

Folt, B., C. P. McGowan, D. A. Steen, S. Piccolomini, M. Hoffman, J. C. Godwin, and C. Guyer. 2020. Modeling strategies and evaluating success during repatriations of elusive and endangered species. Animal Conservation 23:273–285.

Fouilloux, C. A., G. Garcia-Costoya, and B. Rojas. 2020. Visible implant elastomer (VIE) success in early larval stages of a tropical amphibian species. PeerJ 8:e9630.

Frankham, R. 2008. Genetic adaptation to captivity in species conservation programs. Molecular Ecology 17:325–333.

Franz, R., and L. L. Smith. 1999. Distribution and Status of the Striped Newt and Florida Gopher Frog in peninsular Florida. Florida Game and Fresh Water Fish Commission Nongame Project Report. Florida Game and Fresh Water Fish Commission, Tallahassee, FL.

Gale, A. S. 2000. The Cretaceous world. Pages 4–19 *in* S. J. Culver and P. F. Rawson, editors. Biotic Response to Global Change. First Edition. Cambridge University Press, Cambridge, UK.

Georgia Department of Natural Resources. 2017. Rules and Regulations of the State of Georgia, Subject 391-4-10: Protection of endangered, threatened, rare, or unusual species in Georgia, U.S.A. Office of the Secretary of State of Georgia, Atlanta, GA.

Georgia Department of Natural Resources. 2021. Sandhills WMA: East. https://georgiawildlife.com/sandhills-wma-west.

Georgia Department of Natural Resources. 2024. The Private Lands Program (PLP). https://georgiawildlife.com/privatelandsprogram.

Georgia Department of Transportation. 2023. Fall Line Freeway Fact Sheet.

Germano, J. M., and P. J. Bishop. 2009. Suitability of amphibians and reptiles for translocation. Conservation Biology 23:7–15.

Gibbons, J. W., C. T. Winne, D. E. Scott, J. D. Willson, X. Glaudas, K. M. Andrews, B. D. Todd, L. A. Fedewa, L. Wilkinson, R. N. Tsaliagos, S. J. Harper, J. L. Greene, T. D. Tuberville, B. S. Metts, M. E. Dorcas, J. P. Nestor, C. A. Young, T. Akre, R. N. Reed, K. A. Buhlmann, J. Norman, D. A. Croshaw, C. Hagen, and B. B. Rothermel. 2006. Remarkable amphibian biomass and abundance in an isolated wetland: Implications for wetland conservation. Conservation Biology 20:1457–1465.

Gibbons, M. E., A. M. Ferguson, D. R. Lee, and R. G. Jaeger. 2003. Mother-offspring discrimination in the red-backed salamander may be context dependent. Herpetologica 59:322–333.

Gill, D. E. 1978. Effective population size and interdemic migration rates in a metapopulation of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Evolution 32:839–849.

Gill, D. E. 1979. Density dependence and homing behavior in adult red-spotted newts *Notophthalmus Viridescens* (Rafinesque). Ecology 60:800–813.

Glassberg, D. 2001. Sense of History: The Place of the Past in American Life. University of Massachusetts Press, Amherst, MA.

Goebel, T., M. R. Waters, and D. H. O'Rourke. 2008. The late Pleistocene dispersal of modern humans in the Americas. Science 319:1497–1502.

Goldwasser, L., S. Ferson, and L. Ginzburg. 2000. Variability and measurement error in extinction risk analysis: The Northern Spotted Owl on the Olympic Peninsula. Pages 169–187 *in* S. Ferson and M. Burgman, editors. Quantitative Methods for Conservation Biology. Springer, New York, NY.

Graham, S. P., D. A. Steen, K. T. Nelson, A. M. Durso, and J. C. Maerz. 2010. An overlooked hotspot? Rapid biodiversity assessment reveals a region of exceptional herpetofaunal richness in the southeastern United States. Southeastern Naturalist 9:19–34.

Grant, E. H. C., E. Muths, B. R. Schmidt, and S. O. Petrovan. 2019. Amphibian conservation in the Anthropocene. Biological Conservation 236:543–547.

Greer, B. K., S. D. Kirkland, and M. Healey. 2015. A Historical Context of the Turpentine (Naval Stores) Industry in the Atlantic and Gulf Coastal Plains of Georgia, South Carolina and Florida. U.S. Department of Defense, Fort Stewart, GA.

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

Gross, I. P., A. E. Wilson, and M. E. Wolak. 2024. The fitness consequences of wildlife conservation translocations: A meta-analysis. Biological Reviews 99:348–371.

Guarisco, H. 2010. The fishing spider genus *Dolomedes* (Araneae: Pisauridae) in Kansas. Transactions of the Kansas Academy of Science 113:35–43.

Guldi, J. 2016. Landscape and place. Pages 68–82 *in* L. Faire and S. Gunn, editors. Research Methods for History. Second Edition. Edinburgh University Press, Edinburgh, Scotland.

Gurevitch, J., G. A. Fox, N. L. Fowler, and C. H. Graham. 2016. Landscape demography: Population change and its drivers across spatial scales. The Quarterly Review of Biology 91:459–485.

Hanberry, B. B., J. M. Stober, and D. C. Bragg. 2023. Documenting two centuries of change in longleaf pine (*Pinus palustris*) forests of the Coastal Plain Province, southeastern USA. Forests 14:1938.

Hanifin, C. T., Y. Kudo, and M. Yotsu-Yamashita. 2022. Chemical ecology of the North American newt genera *Taricha* and *Notophthalmus*. Pages 102–130 *in* A. D. Kinghorn, H. Falk, S. Gibbons, Y. Asakawa, J.-K. Liu, and V. M. Dirsch, editors. Progress in the Chemistry of Organic Natural Products. Springer Nature Switzerland, Cham, Switzerland.

Hanifin, C. T., M. Yotsu-Yamashita, T. Yasumoto, and E. D. Brodie. 1999. Toxicity of dangerous prey: Variation of tetrodotoxin levels within and among populations of the newt *Taricha granulosa*. Journal of Chemical Ecology 25:2161–2175.

Harding, G., R. A. Griffiths, and L. Pavajeau. 2016. Developments in amphibian captive breeding and reintroduction programs. Conservation Biology 30:340–349.

Harper, R. M. 1904. Explorations in the coastal plain of Georgia during the season of 1902. Bulletin of the Torrey Botanical Club 31:9–27.

Harris, R. N. 1987a. Density-dependent paedomorphosis in the salamander *Notophthalmus viridescens dorsalis*. Ecology 68:705–712.

Harris, R. N. 1987b. An experimental study of population regulation in the salamander, *Notophthalmus viridescens dorsalis* (Urodela: Salamandridae). Oecologia 71:280–285.

Harris, R. N., R. D. Semlitsch, H. M. Wilbur, and J. E. Fauth. 1990. Local variation in the genetic basis of paedomorphosis in the salamander *Ambystoma talpoideum*. Evolution 44:1588–1603.

Harris, R. N., T. J. Vess, J. I. Hammond, and C. J. Lindermuth. 2003. Context-dependent kin discrimination in larval four-toed salamanders *Hemidactylium scutatum* (Caudata: Plethodontidae). Herpetologica 59:164–177.

Harrold, C. C. 1939. Georgia archaeology with especial reference to recent investigations in the interior and on the coast. The Georgia Historical Quarterly 23:55–76.

Hartmann, A. M., M. L. Maddox, R. J. Ossiboff, and A. V. Longo. 2022. Sustained *Ranavirus* outbreak causes mass mortality and morbidity of imperiled amphibians in Florida. EcoHealth 19:8–14.

Hartmann, A. M., K. Sash, E. P. Hill, N. M. Claunch, M. L. Maddox, S. McGrath-Blaser, C. C. McKinstry, R. J. Ossiboff, and A. V. Longo. 2024. Partitioning the influence of host specificity in amphibian populations threatened by multiple emerging infectious diseases. Biological Conservation 296:110685.

Hawkins, B., and H. T. Foster. 2003. The Collected Works of Benjamin Hawkins, 1796–1810. University Alabama Press, Tuscaloosa, AL.

Healy, W. R. 1974. Population consequences of alternative life histories in *Notophthalmus v. viridescens*. Copeia 1974:221–229.

Healy, W. R. 1975. Terrestrial activity and home range in efts of *Notophthalmus viridescens*. American Midland Naturalist 93:131.

Hellmann, P. T. 2005. Historical Gazetteer of the United States. Routledge, New York, NY.

Hemperley, M. R. 1973. Indian place names in Georgia. The Georgia Historical Quarterly 57:562–579.

Henrikson, B.-I. 1990. Predation on amphibian eggs and tadpoles by common predators in acidified lakes. Ecography 13:201–206.

Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998:367.

Heppell, S. S., D. T. Crouse, and L. B. Crowder. 2000. Using matrix models to focus research and management efforts in conservation. Pages 148–168 *in* S. Ferson and M. Burgman, editors. Quantitative Methods for Conservation Biology. Springer, New York, NY.

Heynen, N., and M. Ybarra. 2021. On abolition ecologies and making “freedom as a place.” Antipode 53:21–35.

Higgs, E., D. A. Falk, A. Guerrini, M. Hall, J. Harris, R. J. Hobbs, S. T. Jackson, J. M. Rhemtulla, and W. Throop. 2014. The changing role of history in restoration ecology. Frontiers in Ecology and the Environment 12:499–506.

Hill, D. W. 2024. Muscogee (Creek) Nation Fourth Quarterly Report (FY 2024). Muscogee (Creek) Nation Executive Branch, Okmulgee, OK.

Hoffmann, M. 2024. Rural residents say they are fed up with crop farms turning into solar farms, bringing noise. https://www.wsaz.com/2024/09/16/rural-residents-say-they-are-fed-up-with-crop-farms-turning-into-solar-farms-bringing-noise/.

Houston, M. L., editor. 1929. Reprint of Official Register of Land Lottery of Georgia, 1827. Walton-Forbes Co., Columbus, GA.

Howard, E. 2004. The Taylor County High School prom of 2003. Perspectives in Learning 5:15–19.

Howard, J. S., and J. C. Maerz. 2021. Review and synthesis of estimated vital rates for terrestrial salamanders in the family Plethodontidae. Ichthyology & Herpetology 109:929–939.

Hudson, A. P. 2010. Creek Paths and Federal Roads: Indians, Settlers, and Slaves and the Making of the American South. University of North Carolina Press, Chapel Hill, NC.

Hurlbert, S. H. 1970. Predator responses to the vermilion-spotted newt (*Notophthalmus viridescens*). Journal of Herpetology 4:47–55.

ICON. 2023. ICON core research principles and criteria. Pages 15–17 Integrative Conservation (ICON) PhD Program Handbook.

Jenkins, C. N., K. S. Van Houtan, S. L. Pimm, and J. O. Sexton. 2015. US protected lands mismatch biodiversity priorities. Proceedings of the National Academy of Sciences 112:5081–5086.

Jennison, W. W. 2012. Cultivating Race: The Expansion of Slavery in Georgia, 1750-1860. University Press of Kentucky, Lexington, KY.

Jensen, J. B., and N. Klaus. 2004. *Notophthalmus perstriatus* (Striped Newt) geographic distribution. Herpetological Review 35:403.

Johnson, C. Y. 1998. A consideration of collective memory in African American attachment to wildland recreation places. Human Ecology Review 5:5–15.

Johnson, C. Y., and J. M. Bowker. 2004. African-American wildland memories. Environmental Ethics 26:57–75.

Johnson, S. 2001. Life history, ecology, and conservation genetics of the striped newt (*Notophthalmus perstriatus*). University of Florida, Gainesville, FL.

Johnson, S. A. 2002. Life history of the Striped Newt at a north-central Florida breeding pond. Southeastern Naturalist 1:381–402.

Johnson, S. A. 2003. Orientation and migration distances of a pond-breeding salamander (*Notophthalamus perstriatus*, Salamandridae). Alytes 21:3–22.

Johnson, S. A. 2005. Conservation and life history of the striped newt: The importance of habitat connectivity. Pages 91–98 *in* W. E. Meshaka and K. J. Babbitt, editors. Amphibians and reptiles: Status and conservation in Florida. Krieger Publishing, Malabar, FL.

Johnson, T. A. 2017. African American archival resources: Representation in North Carolina, South Carolina, and Georgia. SLIS Connecting 6:37–54.

Jones, J. R., and T. Landess. 1967. Portraits of Georgia slaves. The Georgia Review 21:126–132.

Jones, M. T., W. R. Milligan, L. B. Kats, T. L. Vandergon, R. L. Honeycutt, R. N. Fisher, C. L. Davis, and T. A. Lucas. 2017. A discrete stage-structured model of California newt population dynamics during a period of drought. Journal of Theoretical Biology 414:245–253.

Jordanova, L. 2016. Approaching visual materials. Pages 31–48 *in* L. Faire and S. Gunn, editors. Research Methods for History. Second. Edinburgh University Press, Edinburgh, Scotland.

Kalezić, M. L., D. D. Cvetković, A. Đorović, and G. V. Džukić. 1996. Alternative life-history pathways: Paedomorphosis and adult fitness in European newts (*Triturus vulgaris* and *T. alpestris*). Journal of Zoological Systematics and Evolutionary Research 34.

Karlsdóttir, B., A. T. Knight, K. Johnson, and J. Dawson. 2021. Lessons from practitioners for designing and implementing effective amphibian captive breeding programmes. Oryx 55:382–392.

Katzner, T. E., J. a. R. Ivy, E. A. Bragin, E. J. Milner-Gulland, and J. A. DeWoody. 2011. Conservation implications of inaccurate estimation of cryptic population size. Animal Conservation 14:328–332.

Keating, L. M., L. Randall, R. Stanton, C. McCormack, M. Lucid, T. Seaborn, S. J. Converse, S. Canessa, and A. Moehrenschlager. 2023. Using decision analysis to determine the feasibility of a conservation translocation. Decision Analysis 20:295–310.

Kennedy, J. C. G. 1864a. Population of the United States in 1860: Compiled from the Original Returns of the Eighth Census Under the Direction of the Secretary of the Interior. Government Printing Office, Washington, D.C.

Kennedy, J. C. G. 1864b. Agriculture of the United States in 1860: Compiled from the Original Returns of the Eighth Census Under the Direction of the Secretary of the Interior. Government Printing Office, Washington, D.C.

Kéry, M., R. M. Dorazio, L. Soldaat, A. Van Strien, A. Zuiderwijk, and J. A. Royle. 2009. Trend estimation in populations with imperfect detection. Journal of Applied Ecology 46:1163–1172.

Kierulff, M. C. M., C. R. Ruiz-Miranda, P. P. de Oliveira, B. B. Beck, A. Martins, J. M. Dietz, D. M. Rambaldi, and A. J. Baker. 2012. The golden lion tamarin *Leontopithecus rosalia*: A conservation success story. International Zoo Yearbook 46:36–45.

King, E. G., and N. Nibbelink. 2019. Challenges of boundary crossing in graduate training for coupled human-natural systems research. Pages 227–264 *in* S. G. Perz, editor. Collaboration Across Boundaries for Social-Ecological Systems Science: Experiences Around the World. Springer International Publishing, Cham, Switzerland.

Kirk, M. A., K. E. Reider, A. C. R. Lackey, S. A. Thomas, and H. H. Whiteman. 2023. The role of environmental variation in mediating fitness trade-offs for an amphibian polyphenism. Journal of Animal Ecology 92:1815–1827.

Kishida, O., A. Tezuka, A. Ikeda, K. Takatsu, and H. Michimae. 2015. Adaptive acceleration in growth and development of salamander hatchlings in cannibalistic situations. Functional Ecology 29:469–478.

Kissel, A. M., W. J. Palen, P. Govindarajulu, and C. A. Bishop. 2014. Quantifying ecological life support: The biological efficacy of alternative supplementation strategies for imperiled amphibian populations. Conservation Letters 7:441–450.

Klaus, J. M., and R. F. Noss. 2016. Specialist and generalist amphibians respond to wetland restoration treatments. The Journal of Wildlife Management 80:1106–1119.

Kleiman, D. G., K. V. Thompson, and C. K. Baer. 2010. Wild Mammals in Captivity: Principles and Techniques for Zoo Management, Second Edition. University of Chicago Press, Chicago, IL.

Kopecký, O. 2020. Factors affecting the retention of Visible Implant Elastomer (VIE) tags in smooth newts (*Lissotriton vulgaris*) during the breeding period. Brazilian Society of Herpetology 15:41–46.

Kuzmin, S. L. 1991. The ecology and evolution of Amphibian cannibalism. Journal of Bengal Natural History Society 10:11–27.

Lackey, A. C. R., M. P. Moore, J. Doyle, N. Gerlanc, A. Hagan, M. Geile, C. Eden, and H. H. Whiteman. 2019. Lifetime fitness, sex-specific life history, and the maintenance of a polyphenism. The American Naturalist 194:230–245.

Lawson, A. J., B. Folt, A. M. Tucker, F. Erickson, and C. P. McGowan. 2021. Decision context as a necessary component of population viability analysis assessments: response to Chaudhary and Oli 2020. Conservation Biology 35:1683–1685.

Levis, N. A., and D. W. Pfennig. 2019. Phenotypic plasticity, canalization, and the origins of novelty: Evidence and mechanisms from amphibians. Seminars in Cell & Developmental Biology 88:80–90.

Licht, L. E., and K. P. Grant. 1997. The effects of ultraviolet radiation on the biology of amphibians. American Zoologist 37:137–145.

Liknes, G. C., M. D. Nelson, and D. J. Kaisershot. 2013. Historical woodland density of the conterminous United States, 1873. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA. https://doi.org/10.2737/RDS-2013-0006.

Lindenmayer, D. B., T. W. Clark, R. C. Lacy, and V. C. Thomas. 1993. Population viability analysis as a tool in wildlife conservation policy: With reference to Australia. Environmental Management 17:745–758.

Luedtke, J. A., J. Chanson, K. Neam, L. Hobin, A. O. Maciel, A. Catenazzi, A. Borzée, A. Hamidy, A. Aowphol, A. Jean, Á. Sosa-Bartuano, A. Fong G., A. De Silva, A. Fouquet, A. Angulo, A. A. Kidov, A. Muñoz Saravia, A. C. Diesmos, A. Tominaga, B. Shrestha, B. Gratwicke, B. Tjaturadi, C. C. Martínez Rivera, C. R. Vásquez Almazán, C. Señaris, S. R. Chandramouli, C. Strüssmann, C. F. Cortez Fernández, C. Azat, C. J. Hoskin, C. Hilton-Taylor, D. L. Whyte, D. J. Gower, D. H. Olson, D. F. Cisneros-Heredia, D. J. Santana, E. Nagombi, E. Najafi-Majd, E. S. H. Quah, F. Bolaños, F. Xie, F. Brusquetti, F. S. Álvarez, F. Andreone, F. Glaw, F. E. Castañeda, F. Kraus, G. Parra-Olea, G. Chaves, G. F. Medina-Rangel, G. González-Durán, H. M. Ortega-Andrade, I. F. Machado, I. Das, I. R. Dias, J. N. Urbina-Cardona, J. Crnobrnja-Isailović, J.-H. Yang, J. Jianping, J. T. Wangyal, J. J. L. Rowley, J. Measey, K. Vasudevan, K. O. Chan, K. V. Gururaja, K. Ovaska, L. C. Warr, L. Canseco-Márquez, L. F. Toledo, L. M. Díaz, M. M. H. Khan, M. Meegaskumbura, M. E. Acevedo, M. F. Napoli, M. A. Ponce, M. Vaira, M. Lampo, M. H. Yánez-Muñoz, M. D. Scherz, M.-O. Rödel, M. Matsui, M. Fildor, M. D. Kusrini, M. F. Ahmed, M. Rais, N. G. Kouamé, N. García, N. L. Gonwouo, P. A. Burrowes, P. Y. Imbun, P. Wagner, P. J. R. Kok, R. L. Joglar, R. J. Auguste, R. A. Brandão, R. Ibáñez, R. Von May, S. B. Hedges, S. D. Biju, S. R. Ganesh, S. Wren, S. Das, S. V. Flechas, S. L. Ashpole, S. J. Robleto-Hernández, S. P. Loader, S. J. Incháustegui, S. Garg, S. Phimmachak, S. J. Richards, T. Slimani, T. Osborne-Naikatini, T. P. F. Abreu-Jardim, T. H. Condez, T. R. De Carvalho, T. P. Cutajar, T. W. Pierson, T. Q. Nguyen, U. Kaya, Z. Yuan, B. Long, P. Langhammer, and S. N. Stuart. 2023. Ongoing declines for the world's amphibians in the face of emerging threats. Nature 622:308–314.

Lunghi, E., and G. Bruni. 2018. Long-term reliability of Visual Implant Elastomers in the Italian cave salamander (*Hydromantes italicus*). Salamandra 54:283–286.

Malmgren, J. C., and M. Thollesson. 1999. Sexual size and shape dimorphism in two species of newts, *Triturus cristatus* and *T. vulgaris* (Caudata: Salamandridae). Journal of Zoology 249:127–136.

Marco, A., M. Lizana, A. Alvarez, and A. R. Blaustein. 2001. Egg-wrapping behaviour protects newt embryos from UV radiation. Animal Behaviour 61:639–644.

Marion, Z. H., and M. E. Hay. 2011. Chemical defense of the Eastern Newt (*Notophthalmus viridescens*): Variation in efficiency against different consumers and in different habitats. PLOS ONE 6:e27581.

Markman, S., N. Hill, J. Todrank, G. Heth, and L. Blaustein. 2009. Differential aggressiveness between fire salamander (*Salamandra infraimmaculata*) larvae covaries with their genetic similarity. Behavioral Ecology and Sociobiology 63:1149–1155.

Martín, J., and P. López. 2004. Balancing predation risk, social interference, and foraging opportunities in backswimmers, *Notonecta maculata*. acta ethologica 6:59–63.

Marzona, E., D. Seglie, and C. Giacoma. 2004. Sexual dimorphism in body size and life-history traits in a population of *Triturus alpestris alpestris*. Italian Journal of Zoology 71:117–120.

Mathews, F., M. Orros, G. McLaren, M. Gelling, and R. Foster. 2005. Keeping fit on the ark: Assessing the suitability of captive-bred animals for release. Biological Conservation 121:569–577.

May, S. E., K. A. Medley, S. A. Johnson, and E. A. Hoffman. 2011. Combining genetic structure and ecological niche modeling to establish units of conservation: A case study of an imperiled salamander. Biological Conservation 144:1441–1450.

McBride, K. 2023. “Slave” or “enslaved”? https://www.npr.org/sections/publiceditor/2023/12/14/1219329636/slave-or-enslaved.

McCain, C., T. Szewczyk, and K. Bracy Knight. 2016. Population variability complicates the accurate detection of climate change responses. Global Change Biology 22:2081–2093.

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

McDaniel, J., and K. D. Alley. 2005. Connecting local environmental knowledge and land use practices: A human ecosystem approach to urbanization in West Georgia. Urban Ecosystems 8:23–38.

McKelvey, K. S., and D. E. Pearson. 2001. Population estimation with sparse data: the role of estimators versus indices revisited. Canadian Journal of Zoology 79:1754–1765.

Means, D. B. 2007. Life cycles, dispersal, and critical habitat utilization of vertebrates dependent upon small isolated water bodies in the Munson Sandhills and Woodville Karst Plain, Leon County, Florida. Report to the Florida Department of Transportation, Florida State University, Tallahassee, FL.

Means, D. B., R. C. Means, and R. P. M. Means. 2008. Petition to list the striped newt, *Notophthalmus perstriatus*, as a federally threatened species under the Endangered Species Act of 1973. Coastal Plains Institute and Land Conservancy, Tallahassee, FL.

Means, R. C., R. P. M. Means, M. Beshel, R. Mendyk, P. Hill, M. Hoffman, S. Reichling, and B. Summerford. 2017. A Conservation Strategy for the Imperiled Striped Newt (*Notophthalmus perstriatus*) in the Apalachicola National Forest, Florida. Report to the US Forest Service, Tallahassee, FL.

Means, R. C., R. P. M. Means, M. Beshel, R. Mendyk, S. Reichling, and B. Summerford. 2015. A Conservation Strategy for the Imperiled Striped Newt (*Notophthalmus perstriatus*) in the Apalachicola National Forest, Florida. Coastal Plains Institute, Tallahassee, FL.

Means, R. C., R. P. M. Means, D. L. Miller, M. J. Gray, S. A. Johnson, D. B. Means, and R. Brenes. 2011. A Conservation Strategy for the Imperiled Striped Newt (*Notophthalmus perstriatus*) in the Apalachicola National Forest, Florida. Coastal Plains Institute, Tallahassee, FL.

Means, R. C., R. P. M. Means, D. L. Miller, M. J. Gray, S. A. Johnson, D. B. Means, and S. Reichling. 2013. A Conservation Strategy for the Imperiled Striped Newt (*Notophthalmus perstriatus*) in the Apalachicola National Forest, Florida. Coastal Plains Institute, Tallahassee, FL.

Means, R. C., R. P. M. Means, D. L. Miller, M. J. Gray, S. Reichling, S. A. Johnson, D. B. Means, and R. Brenes. 2012. A Conservation Strategy for the Imperiled Striped Newt (*Notophthalmus perstriatus*) in the Apalachicola National Forest, Florida. Coastal Plains Institute and Land Conservancy, Tallahassee, FL.

Means, R. C., R. P. M. Means, S. Reichling, M. Beshel, B. Summerford, S. A. Johnson, and D. B. Means. 2014. A Conservation Strategy for the Imperiled Striped Newt (*Notophthalmus perstriatus*) in the Apalachicola National Forest, Florida. Coastal Plains Institute, Tallahassee, FL.

Mebs, D. 2019. Tetrodotoxin content of Rough-skinned Newts, *Taricha granulosa* (Salamandridae), from their northern distribution range, British Columbia, Canada, and Southeast-Alaska, USA. Salamandra 55:82–88.

Mecham, J. S. 1967. *Notophthalmus perstriatus*. Catalogue of American Amphibians and Reptiles:38.1-38.2.

Mendyk, R. W., and M. Beshel. 2017. Ex situ conservation and recovery efforts for the western striped newt at the Jacksonville Zoo and Gardens. Animal Keepers' Forum 44:302–305.

Meyers, J. 2007. No idle past: Uses of history in the 1830 Indian removal debates. Historian 63:53–66.

Miaud, C. 1993. Predation on newt eggs (*Triturus alpestris* and *T. helveticus*): identification of predators and protective role of oviposition behaviour. Journal of Zoology 231:575–581.

Michaels, C. J., B. F. Gini, and R. F. Preziosi. 2014. The importance of natural history and species-specific approaches in amphibian ex-situ conservation. Herpetological Journal 24:135–145.

Michimae, H., and M. Wakahara. 2001. Factors which affect the occurrence of cannibalism and the broad-headed "cannibal" morph in larvae of the salamander *Hynobius retardatus*. Behavioral Ecology and Sociobiology 50:339–345.

Miller, K. A., T. P. Bell, and J. M. Germano. 2014. Understanding publication bias in reintroduction biology by assessing translocations of New Zealand's herpetofauna: Publication bias in reintroduction biology. Conservation Biology 28:1045–1056.

Miller, K. G., P. J. Sugarman, J. V. Browning, M. A. Kominz, R. K. Olsson, M. D. Feigenson, and J. C. Hernández. 2004. Upper Cretaceous sequences and sea-level history, New Jersey Coastal Plain. GSA Bulletin 116:368–393.

Mitchell, J. C., and C. A. Pague. 2014. Filling gaps in life-history data: Clutch sizes for 21 species of North American anurans. Herpetological Conservation and Biology 9:495–501.

Morin, P. J. 1983. Competitive and Predatory Interactions in Natural and Experimental Populations of *Notophthalmus viridescens dorsalis* and *Ambystoma tigrinum*. Copeia 1983:628–639.

Moser, A., and I. Korstjens. 2018. Series: Practical guidance to qualitative research. Part 3: Sampling, data collection and analysis. The European Journal of General Practice 24:9–18.

Napton, D. E., R. F. Auch, R. Headley, and J. L. Taylor. 2010. Land changes and their driving forces in the Southeastern United States. Regional Environmental Change 10:37–53.

Native Governance Center. 2024. How to Talk about Native Nations: A Guide. https://nativegov.org/resources/how-to-talk-about-native-nations/.

Newman, R. A. 1992. Adaptive plasticity in amphibian metamorphosis. BioScience 42:671–678.

Nichols, J. D., J. E. Hines, J.-D. Lebreton, and R. Pradel. 2000. Estimation of contributions to population growth: A reverse-time capture–recapture approach. Ecology 81:3362–3376.

Nielson, E. 2011. "Go in de wilderness": Evading the "eyes of others" in the slave songs. Western Journal of Black Studies 35:106–117.

Okuyama, T. 2019. Census timing alters stage duration distributions in matrix population models. Ecology and Evolution 9:8500–8508.

Orizaola, G., and F. Braña. 2003. Oviposition behaviour and vulnerability of eggs to predation in four newt species (genus *Triturus*). Herpetological Journal 13:121–124.

Oropeza–Sánchez, M. T., A. Sandoval-Comte, P. García–Bañuelos, P. Hernández–López, and E. Pineda. 2020. Use of visible implant elastomer and its effect on the survival of an endangered minute salamander. Animal Biodiversity and Conservation 43.2:187–190.

Ortega-León, A. M., A. H. Santos-Morales, J. G. Zamora-Abrego, H. A. Pérez-Mendoza, A. M. Ortega-León, A. H. Santos-Morales, J. G. Zamora-Abrego, and H. A. Pérez-Mendoza. 2020. Analysis of the population dynamics of the endangered American crocodile, *Crocodylus acutus* in Paramillo National Natural Park. Marine and Freshwater Research 72:14–25.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical Inference from Capture Data on Closed Animal Populations. Wildlife Monographs:3–135.

Pedrono, M., L. L. Smith, J. Clobert, M. Massot, and F. Sarrazin. 2004. Wild-captive metapopulation viability analysis. Biological Conservation 119:463–473.

Percino-Daniel, R., E. Recuero, E. Vázquez-Domínguez, K. R. Zamudio, and G. Parra-Olea. 2016. All grown-up and nowhere to go: Paedomorphosis and local adaptation in *Ambystoma* salamanders in the Cuenca Oriental of Mexico. Biological Journal of the Linnean Society 118:582–597.

Pesarakloo, A., M. Najibzadeh, and S. J. Mirkamali. 2020. Estimating population size and detection probability of the Lorestan newt, *Neurergus kaiseri* (Schmidt, 1952) using an integrated method. Russian Journal of Ecology 51:570–577.

Pfennig, D. W., and J. P. Collins. 1993. Kinship affects morphogenesis in cannibalistic salamanders. Nature 362:836–838.

Pfennig, D. W., P. W. Sherman, and J. P. Collins. 1994. Kin recognition and cannibalism in polyphenic salamanders. Behavioral Ecology 5:225–232.

Phillips, C. T., and J. N. Fries. 2009. An Evaluation of Visible Implant Elastomer for Marking the Federally Listed Fountain Darter and the San Marcos Salamander. North American Journal of Fisheries Management 29:529–532.

Pickett, S. T. A., and M. J. McDonnell. 1993. Humans as components of ecosystems: A synthesis. Pages 310–316 *in* M. J. McDonnell and S. T. A. Pickett, editors. Humans as Components of Ecosystems: The Ecology of Subtle Human Effects and Populated Areas. Springer-Verlag, New York, NY.

Polis, G. A. 1981. The Evolution and Dynamics of Intraspecific Predation. Annual Review of Ecology and Systematics 12:225–251.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:752–757.

Possingham, H. P., D. B. Lindenmayer, and T. W. Norton. 1993. A framework for the improved management of threatened species based on Population Viability Analysis (PVA). Pacific Conservation Biology 1:39–45.

Price, S. J., R. A. Browne, and M. E. Dorcas. 2012. Resistance and resilience of a stream salamander To supraseasonal drought. Herpetologica 68:312–323.

Prinja, S., N. Gupta, and R. Verma. 2010. Censoring in Clinical Trials: Review of Survival Analysis Techniques. Indian Journal of Community Medicine: Official Publication of Indian Association of Preventive & Social Medicine 35:217–221.

Proser, M., P. Shin, and D. Hawkins. 2005. A Nation's Health at Risk III: Growing Uninsured, Budget Cutbacks Challenge President's Initiative to Put a Health Center in Every Poor County. Special Topics Issue Brief, National Association of Community Health Centers, Washington, D.C.

Pulido, L. 2000. Rethinking environmental racism: White privilege and urban development in southern California. Annals of the Association of American Geographers 90:12–40.

Reed, J. M., L. S. Mills, J. B. Dunning Jr., E. S. Menges, K. S. McKelvey, R. Frye, S. R. Beissinger, M.-C. Anstett, and P. Miller. 2002. Emerging Issues in Population Viability Analysis. Conservation Biology 16:7–19.

Regester, K. J., and M. R. Whiles. 2006. Decomposition Rates of Salamander (*Ambystoma maculatum*) Life Stages and Associated Energy and Nutrient Fluxes in Ponds and Adjacent Forest in Southern Illinois. Copeia 2006:640–649.

Resende, P. S., A. B. Viana–Junior, R. J. Young, and C. S. D. Azevedo. 2020. A global review of animal translocation programs. Animal Biodiversity and Conservation:221–232.

Robert, A., B. Colas, I. Guigon, C. Kerbiriou, J.-B. Mihoub, M. Saint-Jalme, and F. Sarrazin. 2015. Defining reintroduction success using IUCN criteria for threatened species: A demographic assessment. Animal Conservation 18:397–406.

Rodrigues, A. S., V. F. Calsavara, F. I. B. Silva, F. A. Alves, and A. P. M. Vivas. 2018. Use of interval-censored survival data as an alternative to Kaplan-Meier survival curves: studies of oral lesion occurrence in liver transplants and cancer recurrence. Applied Cancer Research 38:16.

Rogers Group. 2023. Georgia Operations. https://rogersgroupincint.com/georgia/.

Rogers, K. B., and T. Banulis. 2003. Repatriation of boreal toads *Bufo boreas* on the Grand Mesa, Colorado. Pages 1–14 *in* C. Loeffler, editor. Conservation plan and agreement for the management and recovery of the southern Rocky Mountain population of the boreal toad (*Bufo boreas boreas*). Boreal Toad Recovery Team, USA.

Rorabaugh, J. C., A. K. Owens, A. King, S. F. Hale, S. Poulin, M. J. Sredl, and J. A. Lemos-Espinal. 2020. Reintroduction of the Tarahumara Frog (*Rana tarahumarae*) in Arizona: Lessons learned. Herpetological Conservation and Biology 15:372–389.

Rosenheim, J. A., and S. J. Schreiber. 2022. Pathways to the density-dependent expression of cannibalism, and consequences for regulated population dynamics. Ecology 103:e3785.

Rothermel, B., S. Walls, J. Mitchell, C. Dodd, L. Irwin, D. Green, V. Vazquez, J. Petranka, and D. Stevenson. 2008. Widespread occurrence of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* in the southeastern USA. Diseases of Aquatic Organisms 82:3–18.

Rot-Nikcević, I., M. L. Kalezić, and G. V. Džukić. 2000. Paedogenesis, life history traits and sexual dimorphism: a case study of the smooth newt, *Triturus vulgaris*, from Pannonia. Folia Zoologica 49.

Rovere, A., P. J. Hearty, J. Austermann, J. X. Mitrovica, J. Gale, R. Moucha, A. M. Forte, and M. E. Raymo. 2015. Mid-Pliocene shorelines of the US Atlantic Coastal Plain — An improved elevation database with comparison to Earth model predictions. Earth-Science Reviews 145:117–131.

Ruiz-Gutiérrez, V., and E. F. Zipkin. 2011. Detection biases yield misleading patterns of species persistence and colonization in fragmented landscapes. Ecosphere 2:art61.

Ryan, B. J. 2022. Analyzing Climate Change and Extreme Weather Event Impacts on Human Migration and Vulnerability in the Southeastern United States (2004 – 2018). Auburn University, Auburn, AL.

Ryan, T. J., and R. D. Semlitsch. 1998. Intraspecific heterochrony and life history evolution: Decoupling somatic and sexual development in a facultatively paedomorphic salamander. Proceedings of the National Academy of Sciences 95:5643–5648.

Salthe, S. N. 1969. Reproductive Modes and the Number and Sizes of Ova in the Urodeles. The American Midland Naturalist 81:467–490.

Santana Cordero, A., M. L. Monteiro Quintana, and L. Hernández Calvento. 2014. Reconstructing the environmental conditions of extinct coastal dune systems using historical sources: The case of the Guanarteme dune field (Canary Islands, Spain). Journal of Coastal Conservation 18:323–337.

Santana-Cordero, A. M., and P. Szabó. 2019. Exploring qualitative methods of historical ecology and their links with qualitative research. International Journal of Qualitative Methods 18:1609406919872112.

Sarrazin, F., and R. Barbault. 1996. Reintroduction: Challenges and lessons for basic ecology. Trends in Ecology & Evolution 11:474–478.

Scheele, B. C., F. Pasmans, L. F. Skerratt, L. Berger, A. Martel, W. Beukema, A. A. Acevedo, P. A. Burrowes, T. Carvalho, A. Catenazzi, I. De la Riva, M. C. Fisher, S. V. Flechas, C. N. Foster, P. Frías-Álvarez, T. W. J. Garner, B. Gratwicke, J. M. Guayasamin, M. Hirschfeld, J. E. Kolby, T. A. Kosch, E. La Marca, D. B. Lindenmayer, K. R. Lips, A. V. Longo, R. Maneyro, C. A. McDonald, J. Mendelson, P. Palacios-Rodriguez, G. Parra-Olea, C. L. Richards-Zawacki, M.-O. Rödel, S. M. Rovito, C. Soto-Azat, L. F. Toledo, J. Voyles, C. Weldon, S. M. Whitfield, M. Wilkinson, K. R. Zamudio, and S. Canessa. 2019. Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. Science 363:1459–1463.

Schmidt, B. R. 2003. Count data, detection probabilities, and the demography, dynamics, distribution, and decline of amphibians. Comptes Rendus Biologies 326:119–124.

Schmolke, A., P. Thorbek, D. L. DeAngelis, and V. Grimm. 2010. Ecological models supporting environmental decision making: a strategy for the future. Trends in Ecology & Evolution 25:479–486.

Schnur, S., C. Maki, and E. Burchfield. 2024. “Farmers need the land”: Georgia’s agricultural future in the patchy Anthropocene. Journal of Rural Studies 107:103259.

Scott, D. E. 1990. Effects of Larval Density in Ambystoma Opacum: An Experiment Large-Scale Field Enclosures. Ecology 71:296–306.

Scott, D. E. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology 75:1383–1396.

Scott, D. E., E. D. Casey, M. F. Donovan, and T. K. Lynch. 2007. Amphibian lipid levels at metamorphosis correlate to post-metamorphic terrestrial survival. Oecologia 153:521–532.

Scott, J. M., D. D. Goble, A. M. Haines, J. A. Wiens, and M. C. Neel. 2010. Conservation-reliant species and the future of conservation. Conservation Letters 3:91–97.

Scott, R. V. 1979. Land use and American railroads in the twentieth century. Agricultural History 53:683–703.

Seddon, P. J. 1999. Persistence without intervention: Assessing success in wildlife reintroductions. Trends in Ecology & Evolution 14:503.

Seddon, P. J., and D. P. Armstrong. 2016. Reintroduction and other conservation translocations: History and future developments. Pages 7–27 *in* D. S. Jachowski, J. J. Millspaugh, P. L. Angermeier, and R. Slotow, editors. Reintroduction of Fish and Wildlife Populations. University of California Press, Oakland, CA.

Segev, O., N. Pezaro, V. Rovelli, O. Rybak, A. R. Templeton, and L. Blaustein. 2019. Phenotypic plasticity and local adaptations to dissolved oxygen in larvae fire salamander (*Salamandra infraimmaculata*). Oecologia 190:737–746.

Seigel, R. A., and C. K. J. Dodd. 2002. Translocations of amphibians: Proven management method or experimental technique? Conservation Biology 16:552–554.

Semlitsch, R. D. 1987. Paedomorphosis in *Ambystoma Talpoideum*: Effects of Density, Food, and Pond Drying. Ecology 68:994–1002.

Semlitsch, R. D. 2002. Critical Elements for Biologically Based Recovery Plans of Aquatic-Breeding Amphibians. Conservation Biology 16:619–629.

Semlitsch, R. D., and J. W. Gibbons. 1985. Phenotypic Variation in Metamorphosis and Paedomorphosis in the Salamander *Ambystoma talpoideum*. Ecology 66:1123–1130.

Semlitsch, R. D., R. N. Harris, and H. M. Wilbur. 1990. Paedomorphosis in *Ambystoma talpoideum*: Maintenance of population variation and alternative life-history pathways. Evolution 44:1604–1613.

Sherrod, R. L. 2011. Into the cotton frontier: The Manning quest for an American Canaan. The Georgia Historical Quarterly 95:356–390.

Shields, E. T., Jr. 2008. Imagining the forest: Longleaf pine ecosystems in Spanish and English writings of the Southeast, 1542–1709. Pages 251–268 *in* T. Hallock, I. Kamps, and K. L. Raber, editors. Early Modern Ecostudies: From the Florentine Codex to Shakespeare. Palgrave Macmillan, New York, NY.

Smith, G. C., M. W. Patterson, and H. R. Trendell. 2000. The demise of the longleaf-pine ecosystem. Southeastern Geographer 40:75–92.

Southerland, H. deLeon, and J. E. Brown. 1989. The Federal Road Through Georgia, the Creek Nation, and Alabama, 1806–1836. The University of Alabama Press, Tuscaloosa, AL.

Southern Environmental Law Center. 2019, May 15. Freedom of Information request reveals quota for cutting endangered species protections. https://www.southernenvironment.org/news-and-press/news-feed/freedom-of-information-request-reveals-quota-for-cutting-endangered-species-protections.

Southern Power. 2020. Butler Solar Farm Fact Sheet.

Stambaugh, M. C., R. P. Guyette, and J. M. Marschall. 2011. Longleaf pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. Journal of Vegetation Science 22:1094–1104.

Starkey, M. 2005. Wilderness, Race, and African Americans: An Environmental History from Slavery to Jim Crow. University of California, Berkeley.

Stephenson, L. W. 1926. Major features in the geology of the Atlantic and Gulf Coastal Plain. Journal of the Washington Academy of Sciences 16:460–480.

Stewart, M. A. 2005. If John Muir had been an agrarian: American environmental history West and South. Environment and History 11:139–162.

Stewart-Fusek, C. 2024. Notice of violations of the Endangered Species Act regarding a determination that protection of the striped newt is not warranted.

Stiggins, G. 2001. Creek Indian history: a historical narrative of the genealogy, traditions and downfall of the Ispocoga or Creek Indian tribe of the Indians. University of Alabama Press, Tuscaloosa, AL.

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

Sullivan, C. J. 2005. Grutter effects: Implications for "re-desegregation" of public education in Georgia? Georgia State University Law Review 22:1031–1058.

Szabó, P. 2010. Why history matters in ecology: An interdisciplinary perspective. Environmental Conservation 37:380–387.

Szabó, P. 2015. Historical ecology: past, present and future. Biological Reviews 90:997–1014.

Szabó, P., and R. Hédl. 2011. Advancing the integration of history and ecology for conservation. Conservation Biology 25:680–687.

Takahashi, M. K., and M. J. Parris. 2008. Life cycle polyphenism as a factor affecting ecological divergence within *Notophthalmus viridescens*. Oecologia 158:23–34.

Tapley, B., K. S. Bradfield, C. Michaels, and M. Bungard. 2015. Amphibians and conservation breeding programmes: Do all threatened amphibians belong on the ark? Biodiversity and Conservation 24:2625–2646.

Tapley, B., K. Johnson, C. J. Michaels, K. Bradfield, D. Barber, L. Randall, K. Vasudevan, C. Paszkowski, R. A. Griffiths, N. E. Calatayud, E. Griffith, and F. Kacoliris. 2024. Conservation breeding. Pages 267–283 *in* S. Wren, A. Borzée, R. Marcec-Greaves, and A. Angulo, editors. Amphibian Conservation Action Plan: A

Status Review and Roadmap for Global Amphibian Conservation. IUCN, Gland, Switzerland.

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

Taylor, B. E., D. E. Scott, and J. W. Gibbons. 2006. Catastrophic Reproductive Failure, Terrestrial Survival, and Persistence of the Marbled Salamander. Conservation Biology 20:792–801.

Thompson, P. D., C. L. Lundskog, and D. E. Dittmer. 2022. A successful reintroduction of Columbia Spotted Frog (*Rana luteiventris*) through repatriation of recently hatched larvae. Ichthyology & Herpetology 110:131–137.

Toone, W. D., and M. P. Wallace. 1994. The extinction in the wild and reintroduction of the California condor (*Gymnogyps californianus*). Pages 411–419 *in* P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, editors. Creative Conservation: Interactive Management of Wild and Captive Animals. Springer Netherlands, Dordrecht.

Toscano, B. J., V. Hin, and V. H. W. Rudolf. 2017. Cannibalism and Intraguild Predation Community Dynamics: Coexistence, Competitive Exclusion, and the Loss of Alternative Stable States. American Naturalist 190:617–630.

Tóth, Z., H. Hoi, and A. Hettyey. 2010. Kin discrimination during egg-cannibalism in smooth newts: does competition matter? Journal of Zoology 284:46–52.

Tracey, J. P., P. J. S. Fleming, and G. J. Melville. 2005. Does variable probability of detection compromise the use of indices in aerial surveys of medium-sized mammals? Wildlife Research 32:245.

Turghan, M. A., Z. Jiang, and Z. Niu. 2022. An update on status and conservation of the Przewalski's horse (*Equus ferus przewalskii*): Captive breeding and reintroduction projects. Animals 12:3158.

Turnbull, B. W. 1976. The Empirical Distribution Function with Arbitrarily Grouped, Censored and Truncated Data. Journal of the Royal Statistical Society: Series B (Methodological) 38:290–295.

U.S. Agricultural Stabilization and Conservation Service, Aerial Photography Division. 1937. Taylor County, 1937: Aerial photography index. image/jp2. 1:20,000. United States, Georgia, Taylor County, 32.55546, -84.25046. Aerial photographs. University of Georgia Libraries, Map and Government Information Library, Athens, GA, presented in the Digital Library of Georgia. https://dlg.usg.edu/record/gyca_gaphind_taylor-1937 [accessed 11 Jan 2023]

U.S. Agricultural Stabilization and Conservation Service, Aerial Photography Division. 1942. Taylor County, 1942: Aerial photography index. image/jp2. 1:20,000.

United States, Georgia, Taylor County, 32.55546, -84.25046. Aerial photographs. University of Georgia Libraries, Map and Government Information Library, Athens, Ga. Library reference designation, as presented in the Digital Library of Georgia. https://dlg.usg.edu/record/gyca_gaphind_taylor-1942 [accessed 11 Jan 2023]

U.S. Agricultural Stabilization and Conservation Service, Aerial Photography Division. 1958. Taylor County, 1958: Aerial photography index. image/jp2. 1:20,000. United States, Georgia, Taylor County, 32.55546, -84.25046. Aerial photographs. University of Georgia Libraries, Map and Government Information Library, Athens, GA, presented in the Digital Library of Georgia. https://dlg.usg.edu/record/gyca_gaphind_taylor-1958 [accessed 11 Jan 2023]

U.S. Agricultural Stabilization and Conservation Service, Aerial Photography Division. 1965. Taylor County, 1965: Aerial photography index. image/jp2. 1:20,000. United States, Georgia, Taylor County, 32.55546, -84.25046. Aerial photographs. University of Georgia Libraries, Map and Government Information Library, Athens, GA, presented in the Digital Library of Georgia. https://dlg.usg.edu/record/gyca_gaphind_taylor-1965 [accessed 11 Jan 2023]

U.S. Agricultural Stabilization and Conservation Service, Aerial Photography Division. 1971. Taylor County, 1971: Aerial photography index. image/jp2. 1:20,000. United States, Georgia, Taylor County, 32.55546, -84.25046. Aerial photographs. University of Georgia Libraries, Map and Government Information Library, Athens, GA, presented in the Digital Library of Georgia. https://dlg.usg.edu/record/gyca_gaphind_taylor-1971 [accessed 11 Jan 2023]

U.S. Agricultural Stabilization and Conservation Service, Aerial Photography Division. 1977. Taylor County, 1977: Aerial photography index. image/jp2. 1:20,000. United States, Georgia, Taylor County, 32.55546, -84.25046. Aerial photographs. University of Georgia Libraries, Map and Government Information Library, Athens, GA, presented in the Digital Library of Georgia. https://dlg.usg.edu/record/gyca_gaphind_taylor-1977 [accessed 11 Jan 2023]

U.S. Census Bureau. 2018. Cartographic Boundary Files: States.

U.S. Census Bureau. 2020a. Total population, Decennial Census, DEC Demographic and Housing Characteristics, Table P1. https://data.census.gov/table/DECENNIALDHC2020.P1?g=160XX00US1312120

U.S. Census Bureau. 2020b. Total population, Decennial Census, DEC Demographic and Housing Characteristics, Table P1. https://data.census.gov/table/DECENNIALDHC2020.P1?q=Taylor County, Georgia.

U.S. Fish & Wildlife Service. 2011. Endangered and threatened wildlife and plants: 12-month finding on a petition to list the striped newt as threatened. Federal Register 76:32911–32929.

U.S. Fish & Wildlife Service. 2018. Endangered and threatened wildlife and plants: 12-month findings on petitions to list 13 species as endangered or threatened species. Federal Register 83:65127–65134.

USDA Forest Service, G. S. and T. C. 2018. Tribal Land Cessions in the United States.

Vaissi, S., and M. Sharifi. 2016. Variation in food availability mediate the impact of density on cannibalism, growth, and survival in larval yellow spotted mountain newts (*Neurergus microspilotus*): Implications for captive breeding programs. Zoo Biology 35:513–521.

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

Vignoli, L., F. Velletrani, C. Venditti, L. Luiselli, Y. Yadid, and D. Macale. 2018. Short, medium and long-term effects of density on the demographic traits of a threatened newt. Ecological Research 33:1039–1048.

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

Walker, M. 2021. The importance of the turpentine industry in the American South. Academia Letters 4512:1–5.

Wallenstein, P. 1976. From Slave South to New South: Taxes and spending in Georgia from 1850 through Reconstruction. The Journal of Economic History 36:287–290.

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

Walls, S. C., and A. R. Blaustein. 1995. Larval marbled salamanders*, Ambystoma opacum*, eat their kin. Animal Behaviour 50:537–545.

Walls, S. C., and R. E. Roudebush. 1991. Reduced Aggression Toward Siblings as Evidence of Kin Recognition in Cannibalistic Salamanders. The American Naturalist 138:1027–1038.

Walsh, J. C., L. V. Dicks, and W. J. Sutherland. 2015. The effect of scientific evidence on conservation practitioners' management decisions. Conservation Biology 29:88–98.

Webster, G. R., and J. Bowman. 2008. Quantitatively delineating the Black Belt geographic region. Southeastern Geographer 48:3–18.

Weiman, D. F. 1991. Peopling the land by lottery? The market in public lands and the regional differentiation of territory on the Georgia frontier. The Journal of Economic History 51:835–860.

Wells, K. D. 2007. The Ecology & Behavior of Amphibians. University of Chicago Press, Chicago, IL.

Wharton, C. H. 1978. The Natural Environments of Georgia. Georgia Department of Natural Resources, Atlanta, GA.

Wharton, C. H. 1989. The Natural Environments of Georgia. Georgia Department of Natural Resources, Environmental Protection Division, Geologic Survey Branch, Atlanta, GA.

White, G. C. 2000. Population Viability Analysis: Data Requirements and Essential Analyses. Page 288 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York.

Whiteman, H. H. 1994. Evolution of facultative paedomorphosis in salamanders. The Quarterly Review of Biology 69:205–221.

Whiteman, H. H., S. A. Wissinger, and W. S. Brown. 1996. Growth and foraging consequences of facultative paedomorphosis in the tiger salamander, *Ambystoma tigrinum nebulosum*. Evolutionary Ecology 10:433–446.

Whiteman, H. H., S. A. Wissinger, M. Denoël, C. J. Mecklin, N. M. Gerlanc, and J. J. Gutrich. 2012. Larval growth in polyphenic salamanders: Making the best of a bad lot. Oecologia 168:109–118.

Whiterod, N. S., C. R. Todd, S. Zukowski, S. M. C. Raymond, M. Asmus, and M. J. Todd. 2020. A population model provides support for management decisions, enables ongoing research and reinforces strong partnerships to manage a threatened freshwater crayfish. Aquatic Conservation: Marine and Freshwater Ecosystems 30:1836–1840.

Wilbur, H. M. 1980. Complex Life Cycles. Annual Review of Ecology and Systematics 11:67–93.

Wilbur, H. M. 1997. Experimental Ecology of Food Webs: Complex Systems in Temporary Ponds. Ecology 78:2279–2302.

Wilbur, H. M., and J. P. Collins. 1973. Ecological Aspects of Amphibian Metamorphosis: Nonnormal distributions of competitive ability reflect selection for facultative metamorphosis. Science 182:1305–1314.

Wildy, E. L., D. P. Chivers, J. M. Kiesecker, and A. R. Blaustein. 1998. Cannibalism Enhances Growth in Larval Long-Toed Salamanders (*Ambystoma macrodactylum*). Journal of Herpetology 32:286–289.

Wildy, E. L., D. P. Chivers, J. M. Kiesecker, and A. R. Blaustein. 2001. The effects of food level and conspecific density on biting and cannibalism in larval long-toed salamanders, *Ambystoma macrodactylum*. Oecologia 128:202–209.

Wilson, B. H. 1925. Telegraph pioneering. The Palimpsest 6:373–393.

Winne, C. T., and T. J. Ryan. 2001. Aspects of Sex-Specific Differences in the Expression of an Alternative Life Cycle in the Salamander *Ambystoma talpoideum*. Copeia 2001:143–149.

Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: Estimating vital-rate effects on population growth for conservation. Ecology 81:628–641.

Woodward, T. S. 1859. Woodward's reminiscences of the Creek or Muscogee Indians, contained in letters to friends in Georgia and Alabama. Barrett & Wimbish, Montgomery, AL.

Yotsu-Yamashita, M., J. Gilhen, R. W. Russell, K. L. Krysko, C. Melaun, A. Kurz, S. Kauferstein, D. Kordis, and D. Mebs. 2012. Variability of tetrodotoxin and of its analogues in the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Urodela: Salamandridae). Toxicon 59:257–264.

You, H., Y. Liu, and K. Fujiwara. 2013. Effects of life-history components on population dynamics of the rare endangered plant *Davidia involucrata* 2013.

Zhang, L., W. Jiang, Q.-J. Wang, H. Zhao, H.-X. Zhang, R. M. Marcec, S. T. Willard, and A. J. Kouba. 2016. Reintroduction and post-release survival of a living fossil: The Chinese giant salamander. PLOS ONE 11:e0156715.

Zhang, Y., I. Majumdar, and J. Schelhas. 2010. Changes in woodland use from longleaf pine to loblolly pine. Sustainability 2:2734–2745.

Zhigang, J., and Z. Hao. 2019. Reintroduction of the Przewalski's horse in China: Status quo and outlook. Nature Conservation Research 4:15–22.

Zúñiga-Vega, J. J., F. R. Méndez-de la Cruz, and O. Cuellar. 2008. Demography of the lizard *Sceloporus grammicus*: Exploring temporal variation in population dynamics. Canadian Journal of Zoology 86:1397–1409.