HABITAT RESTORATION AND TRANSLOCATION FOR THREATENED AMPHIBIANS IN GEORGIA

by

JADE SAMPLES

(Under the Direction of John C. Maerz and Lora L. Smith)

Seasonal wetlands of the Coastal Plain have been severely degraded. These wetlands are critical breeding habitats for many amphibians. We monitored amphibian communities in restored and non-restored wetlands across four managed landscapes in Georgia. We fit an integrated Bayesian community occupancy model to evaluate amphibian responses to wetland conditions. Amphibian responses were species-specific and dependent on prior occupancy patterns. The results highlight the importance of landscape context and long-term monitoring to reduce uncertainty about wetland restoration efforts and management decisions, including translocations of priority species. We used soft-release enclosures to evaluate stocking density effects on survival and paedotypy for captive-reared Striped Newts. There was evidence of positive effects of larval body size at release on survival. Most larvae developed into paedotypic adults within two months. Our results indicate that release of larger, late-stage larvae can enhance post-release survival, promote paedotypy, and facilitate early reproduction of Striped Newts.

INDEX WORDS: Habitat Restoration, Herpetofauna, Translocation, Wetlands, Wildlife Management, Hierarchical Occupancy Model, Adaptive Management

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DEDICATION

"What is there to life if a man cannot hear the lovely cry of the whippoorwill

or the arguments of the frog around the pond at night?"

— Chief Seattle

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

North American wildlife management is an evolving discipline shaped by shifting cultural and societal values. Indigenous communities practiced forms of land and resource stewardship long before European colonization. By the early 20th century, management was primarily defined by habitat manipulation to produce sufficient game for recreational hunting (Geist et al., 2001). More contemporary definitions broaden the scope of management to include the manipulation of wildlife populations and their habitats to meet goals valued by diverse stakeholders (Riley et al., 2002). This transition reflects a shift from a narrow focus on game species management to broader biodiversity conservation as wildlife populations decline worldwide at unprecedented speed (Manfredo et al., 2021). Wildlife management can no longer exclusively rely on expert authority and scientific principles to guide decisions but must recognize the complexity of managing wildlife as a public trust (Manfredo et al., 2021; Riley et al., 2002). The North American Model of Wildlife Conservation characterizes this responsibility as a "three-legged stool", integrating habitat management, population management, and people (Yarrow, 2009).

Habitat Management

Habitat management is often regarded as the primary of the three pillars, as habitat loss and degradation are by far the largest contributors to wildlife population declines and extinctions (Hylander & Ehrlén, 2013). These factors can also indirectly lead to the decline of remaining populations, even in well-managed landscapes, through the erosion of metapopulation processes (Hanski & Ovaskainen, 2002; Schnell et al., 2013). Habitat loss coupled with fragmentation can reduce connectivity among remnant habitat patches, leading to reduced dispersal rates among patches. Dispersal is critical for demographic and genetic rescue of populations. Extinctions in remnant degraded or isolated patches are seldom instantaneous but rather lag, creating what is known as an extinction debt (Semlitsch et al., 2017). However, the phenomenon of extinction debt and lagging population declines creates the opportunity to use habitat restoration and other population interventions to stabilize and recover populations before extinctions occur (Kuussaari et al., 2009; Vellend et al., 2006). Restoring degraded habitats can increase target species' abundance and improve connectivity between fragmented habitats and populations.

That habitat restoration should lead to increased species' abundance and persistence seems so self-evident that it can lead to unrealistic or undefined expectations and ineffective conservation outcomes. Implicit in many restoration projects is "The Field of Dreams Hypothesis" (Frick et al., 2014; Palmer et al., 2016), which assumes that: (1) habitat loss was the primary driver of the original population declines and, therefore, (2) there is a direct relationship between key habitat attributes (e.g., plant community composition and structure, wetland hydroperiod, disturbance regime, etc.) and the presence and abundance of a target species, and (3) species can and will naturally find and recolonize restored areas without additional management interventions (e.g., translocations). In practice, such relationships are more complex and therefore the effects of habitat management actions are often nonlinear in time or space (Brown et al., 2023; Hilderbrand et al., 2005).

The implicit objectives of habitat restoration are to increase patch quality and decrease distance between patches. Colonization and population growth within restored habitats will lag following restoration depending on the species and the degree of isolation from potential source populations (Brown et al., 2023). In managed landscapes, rare species often persist as a network of patchy, remnant populations. The persistence of these networks, or metapopulations, depends on patch quality, patch distance, and the interaction of landscape structure with species-specific traits such as dispersal capacity (Brooks et al., 2002; Hanski & Ovaskainen, 2000; Tilman et al., 1994). For dispersal-limited species, restored habitat may remain uncolonized for a considerable time without intervention. Thus, preserving metapopulation processes in fragmented landscapes requires not only an understanding of both patch quality and distribution, but also of a species' ability to recolonize after restoration (Bulman et al., 2007).

Another reason for the lag in time or failure of a species to recolonize restored habitat patches can be related to limitations in our ability to fully restore all the required elements for an area to support a species. Ecosystems that have evolved over millennia cannot easily be restored on a scale of years to decades (Hilderbrand et al., 2005; Hobbs & Norton, 1996). Therefore, restoration efforts may not meet the needs of some species over time scales relevant to managers. Historic land use, the complexity of managed landscapes, and the irreversible nature of some habitat loss further constrain species-specific outcomes (Yepsen et al., 2014). Overreliance on the Field of Dreams Hypothesis risks overlooking the need for more direct management interventions such as translocations or addressing genetic bottlenecks to bolster populations.

Direct Population Management

Translocation of wild or captive-bred animals is a common tool paired with habitat restoration to supplement or re-establish wild populations (Seddon et al., 2007). Evaluations of these release programs have yielded mixed results and many sources of bias cloud our understanding of the success of translocations (Gould et al., 2023; Miller et al., 2014). While it seems intuitive that the ultimate goal of translocations is to establish self-sustaining populations, members of the 7th World Conference on Breeding Endangered Species (Seddon, 1999) cautioned that this definition of success is problematic and proposed that the success of translocations be evaluated in short to longer term milestones: (1) survival of the release generation; (2) breeding by the release generation and their offspring; (3) persistence of the re-established population, perhaps assessed through population viability analysis. Resource availability and habitat quality are both recognized as key influences on success on translocations, however, a lack of knowledge of biological constraints imposed on populations such as density dependent processes and dispersal limitations also influence the persistence of translocated populations (Converse et al., 2013; Dodd & Seigel, 1992; Folt et al., 2019; Gould et al., 2023). Focal species for translocation projects are often rare, thus poorly studied, leading to uncertainties regarding the presence of limiting life history traits and low detection probabilities following release (Folt et al., 2019; Wendt et al., 2021). Therefore, more work is needed to understand the influence of biological constraints for translocated organisms and in managed ecosystems through targeted monitoring and release strategies.

Decision-Making

Effective conservation requires collaborative effort and explicit evaluation of whether management actions accomplish intended goals and adaptation when they do not. Adaptive management provides a structured, iterative framework that integrates monitoring and learning into decision-making (Williams & Brown, 2018). Central to this framework is the learning loop: defining the problem, setting objectives, implementing actions, monitoring outcomes, and adjusting strategies accordingly (Canessa et al., 2019). Management inherently involves uncertainty. By linking management actions to measurable objectives such as target occupancy of focal species, population sizes, or measures of recruitment over defined spatial and temporal scales, managers can reduce uncertainty and refine methodologies for future decisions. In habitat restoration and species translocation projects, data on baseline states is often limited and reported outcomes for target communities are frequently anecdotal (Armstrong & Seddon, 2008; Seddon et al., 2007). Without focused monitoring plans and measurable objectives, it is difficult to assess whether restoration or translocations are successful and what variables are most important to the outcome (Peyre et al., 2001, Romesburg, 1981). Applying adaptive management to these efforts can ensure that monitoring informs iterative adjustments and supports evidence-based conservation practices.

Geographically Isolated Wetlands

The longleaf pine (*Pinus palustris*) and wiregrass (*Aristida stricta*) ecosystem supports a high level of regional biodiversity (Kirkman et al., 1999). Over 1,200 species of plants and wildlife are associated with this ecosystem (USDA NRCS). Longleaf pine ecosystems have been reduced to only 3% of the historic range, which once encompassed over 36 million ha (Ojha et al., 2021). Many former Longleaf pine systems have experienced soil disturbance from agricultural and silvicultural practices, fire suppression and the associated woody encroachment, and invasions by nonnative species (Stuber et al., 2016). Recent conservation and restoration efforts have roughly doubled the amount of Longleaf pine stands to ~ 6% of the historic range (NRCS, 2023), which over the long term will benefit terrestrial species such as the Red-cockaded woodpecker (*Leuconotopicus borealis*) and the Gopher tortoise (*Gopherus polyphemus*). However, many species associated with Longleaf pine ecosystems depend on geographically isolated wetlands (GIWs) embedded within these terrestrial landscapes. Thus, there is potentially high conservation value to restoring GIWs as well as Longleaf pine. The widespread loss and degradation of GIWs is particularly detrimental to the amphibians that rely on them for reproduction (Klaus & Noss, 2016; Lance & Pechmann, 2024; Snodgrass et al., 2000; Tiner, 2003). Recent GIW restoration efforts have targeted plant communities, connectivity, and hydrology, with limited focus on their effectiveness for wildlife (Golden et al., 2017; K. L. Martin & L. K. Kirkman, 2009).

Priority Amphibians of the Southeastern Coastal Plains

Many amphibian species in the Southeastern Coastal Plain are reliant on GIWs to support breeding populations. Thirteen amphibian species are exclusively associated with Longleaf pine uplands and GIWs (Means 2007, Smith et al., 2017). Five amphibians considered "Species of Greatest Conservation Need (SGCN)" in Georgia according to the 2025 State Wildlife Action Plan (SWAP) are Longleaf pine and GIW specialists. These include the Frosted Flatwoods Salamander (*Ambystoma cingulatum*), Reticulated Flatwoods Salamander (*Ambystoma bishopi*), Gopher Frog (*Rana capito*), and the Striped Newt (*Notophthalmus perstriatus*). The Eastern Tiger Salamander (*Ambystoma tigrinum*) and Ornate Chorus Frog (*Pseudacris ornata*) are also recognized as species of conservation interest due to apparent population declines (Koen et al., 2025). Reticulated and Frosted Flatwoods Salamanders are federally protected. While the Gopher Frog and the Striped Newt are currently under review for federal listing, both species are currently protected under Georgia's Endangered Wildlife Act of 1973 (Georgia Code § 27-3-130, 1973) and Georgia Rules & Regulations (Ga. Comp. R. & Regs. r. 391-4-10-.01) and are considered Species of Highest Conservation Concern. The Eastern Tiger Salamander and Ornate Chorus Frog currently have no legal protections in Georgia (Georgia Code § 27-1-28, 2024). The

Eastern Tiger Salamander is considered a data deficient species in Georgia as little is known about their conservation status in the state. The Ornate Chorus Frog, though once considered a common species, has seen abrupt declines and extirpations since the 1990's and has been included in four southeastern states' SWAPs (Burrow, 2022; Koen et al., 2025).

Amphibian declines in the southeast are likely not driven by a single threat, but rather by the interaction of multiple stressors (Grant et al. 2016; Luedtke et al., 2023), including the loss of quality uplands and breeding wetlands from intensive agriculture and silviculture (Stuber et al., 2016), fire suppression (Martin and Kirkman, 2009), and increasing drought frequency (Hossack et al., 2013; KC et al., 2015). Modern forestry practices and the replacement of Longleaf pine with Loblolly pine (*Pinus taeda*) coupled with fire exclusion have degraded remaining wetland habitat and altered wetland hydrology (Matusick et al., 2020; Nowacki and Abrams, 2008). One such practice is the ditching and draining of wetlands for agriculture or pine plantations. Ditching significantly reduces the hydroperiod which hinders larval amphibian development prior to metamorphosis (Brannelly et al., 2019; Sun et al., 2001). The combination of these stressors has resulted in the occurrence of suitable upland and wetland habitat becoming increasingly rare. Climate change has further exacerbated declines as prolonged droughts become more frequent, shorten hydroperiods, and increase risk of local extirpation (Hossack et al., 2013; KC et al., 2015). Historically, habitat connectivity would have facilitated demographic rescue and recolonization after stochastic local extinction (Pulliam, 1988). However, habitat loss, fragmentation, and degradation from fire suppression and challenges associated with burning wetlands during the growing season have reduced connectivity, increasing the likelihood that local populations will be extirpated without recolonization from source populations (Means et al., 2004; Schurbon & Fauth, 2003; Schurbon & Fauth, 2004).

The Striped Newt is among the many imperiled species in the southern Coastal Plains of Georgia that rely heavily on GIWs embedded within xeric longleaf pine savannas (Dodd Jr & Laclaire, 1995). In Georgia, the Striped Newt is state-threatened with only four or fewer extant populations remain in Georgia (Georgia SWAP, 2025; Farmer et al., 2017), and only one robust population currently known and restricted to a single wetland on a state-owned Wildlife Management Area (Navis, 2025). Most other known populations on public or privately managed conservation lands are either likely extirpated or exist at very low abundance, such that they are highly vulnerable to stochastic extinction (Farmer et al., 2017). The main driver of Striped Newt declines is presumed to be habitat loss, particularly the conversion and use of terrestrial habitats around wetlands for intensive forestry or agriculture and the draining or degradation of GIWs (Farmer et al., 2017). However, Striped Newt populations continue to decline and go extinct on large, managed landscapes. The causes of these Striped Newt population declines remain unclear but may be connected to disruption of metapopulation dynamics, habitat degradation, and climate change. Striped Newts population dynamics appear particularly sensitive to wetland hydroperiod and canopy closure, thus it is presumed that continued declines on managed landscapes have been driven by remnant wetland habitat degradation and increasing drought frequency (Dodd, 1993; Farmer et al., 2017; Johnson 2002).

In response to the precarious status of Striped Newts, state agencies and numerous conservation organizations have developed captive-breeding programs using wild-caught founders, with the goal of releasing captive-produced Striped Newts into restored wetlands within their historic range (Georgia SWAP, 2025). The long-term success of these initiatives will depend on addressing ecological uncertainties and refining release strategies through targeted monitoring and research. Striped Newts have a particularly complex life cycle that is environmentally and density dependent, making their captive rearing and translocations challenging (Navis, 2025). Success of previous Striped Newt translocations in Florida has been difficult to assess because newts were released directly into wetlands (hard releases). These releases have yielded very few detections of newts, and it cannot be determined whether this reflects mortality, emigration, or low detection (R. Means, personal communication, 2024).

Work by Navis and Maerz (Navis, 2025) has shown that in natural wetlands with longer hydroperiods in Georgia, Striped Newt larvae tended to develop into paedotypic adults that breed within their first year, driving rapid recruitment and population growth following pond drying events. This process is likely critical to sustaining robust newt populations and suggests that the release of intermediate to late-stage larvae may be more effective for establishing populations. Collaborators at the Atlanta Botanical Garden have improved the husbandry of captive-reared newts such that they can produce later stage Striped Newt larvae that retain their gills. However, it is unknown whether these larvae will remain paedotypic after translocation. In addition, it is unknown whether there are density-dependent effects on translocation success. Amphibians with complex life cycles often exhibit strong density-dependence, particularly within aquatic larval or adult life stages (Gill, 1979; Petranka, 1989). Stocking Striped Newts at low densities may lead to negative effects on recruitment or increased stochastic failure (Allee effects). Alternatively, the use of "soft-release" strategies such as stocking animals temporarily into pens or cages in restored habitats could improve Striped Newt survival and recruitment while facilitating post-release monitoring. However, stocking at high densities might increase competition among larvae, reducing their fitness or triggering them into developmental pathways that do not yield rapid population growth. In Broken-Striped Newts (*Notophthalmus viridescens doralis*), larval density impacts growth, sexual maturity, and life-history form (Harris, 1987), but no such data from *in situ* studies exists for Striped Newts. The evaluation effects of soft release strategies and stocking densities on the development and reproduction of captive-bred Striped Newts could substantially improve management objectives.

Thesis Objectives

The objectives of this thesis were to (1) estimate the near-term effects of wetland restoration and other factors on amphibian occupancy within geographically isolated wetlands among three managed landscapes in Georgia, and (2) evaluate the effect of stocking density on larval survival and reproductive success of captive-bred Striped Newt (*Notophthalmus perstriatus*) following translocation at a restored wetland. This thesis is divided into four chapters (including this introduction). Chapters 2 and 3 are written as manuscripts intended for publication. Chapter 2 presents a multi-year study monitoring the changes in amphibian communities at 55 restored and non-restored wetlands across four landscapes in Georgia. I estimated amphibian community occupancy and richness at historic, unrestored, and restored wetlands of various ages. Using an integrated Bayesian community occupancy model, I estimated the effects of canopy cover, hydroperiod, and distance to the nearest occupied wetlan on amphibian occupancy probabilities. Chapter 3 describes an adaptive management experiment translocating captive-bred Striped Newts to a restored wetland on the Jones Center at Ichauway using a soft-release methodology. I experimentally investigate release density influence on reproductive success of captive-reared Striped Newts in the wild. Additionally, I estimated whether current soft-release methods meet the criteria for “successful” translocations as defined by Seddon (2010). Chapter 4 summarizes the findings of the thesis and discusses potential applications of the findings for pairing wetland restorations with informed translocations.

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CHAPTER 2

MODELING AMPHIBIAN OCCUPANCY RESPONSES TO WETLAND CONDITIONS FOR RESTORATION IN GEORGIA WETLANDS[1]

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[1] Samples, J.A., L.L. Smith, E.O. Kerr, M. Cinello-Smith, K. Hefferle, V. M. Terrell, and J.C. Maerz. To be submitted to a peer-reviewed journal.

Abstract

Seasonally inundated, geographically isolated wetlands (GIWs) of the Southeastern Coastal Plain have experienced extensive degradation due to altered hydrology, fire suppression, and associated encroachment of woody vegetation. These wetlands are critical breeding habitats for many endemic amphibians, including the state-threatened Gopher Frog (*Rana capito*) and Striped Newt (*Notophthlamus perstriatus*). Restoration of these isolated wetlands is an important opportunity to conserve regional biodiversity. Wetland restoration efforts have primarily focused on restoring plant communities and hydrology of GIWs, but there is limited information on the effectiveness of restoration on target wildlife species. From 2019-2024, we conducted post-restoration monitoring of amphibian and vegetation structure across four managed landscapes in Georgia, covering more than 50 wetlands in varying stages of management. We used a combination of acoustic recording devices and dipnet surveys to assess amphibian occurrence and post-restoration vegetation surveys and characterize pre- and post-restoration conditions. We predicted that responses to site covariates would be species-specific, but that amphibian occupancy would generally increase decreasing canopy cover, increasing hydroperiod, and decreased distance to the nearest occupied wetland. We analyzed the data using an integrated Bayesian hierarchical community occupancy model to evaluate species-specific responses to three site covariates: canopy cover, hydroperiod, and distance to nearest occupied wetland. There was evidence of species-specific differences in occupancy in relation to hydroperiod and a generally negative relationships between amphibian occupancy and increased canopy cover and increased distance. Most relationships between amphibian occupancy and site covariates had high uncertainty and varied among landscapes. The results of this study indicated that near-term responses of amphibian occupancy to wetland conditions are highly uncertain, likely to be

species-specific and depend on prior occupancy patterns among managed landscapes. To reduce uncertainty about wetland restoration efforts and make more informed management decisions – including identifying additional management actions needed to complement habitat restoration – there is a clear need to continue targeted, longer-term monitoring. Additional management actions such as translocations of priority species using an explicit adaptive restoration framework should be considered to maximize the chance of restoring threatened amphibians.

Introduction

Habitat loss and degradation are the largest contributors to wildlife population declines and extinctions (Hylander & Ehrlén, 2013). These factors can also indirectly lead to the decline of remaining populations, even in well-managed landscapes, through the erosion of metapopulation processes (Hanski & Ovaskainen, 2002; Schnell et al., 2013). Populations of threatened species that persist in degraded or isolated habitats are highly vulnerable to local extinction. Extinctions in degraded or isolated patches are seldom instantaneous, but rather populations experience a time lag in declines, creating what is known as an extinction debt (Semlitsch et al., 2017). Extinction debts occur when species persist for some time in habitat that is no longer sufficient to support a population long-term. However, the phenomenon of extinction debt and lagging population declines creates the opportunity to use habitat restoration and other population interventions to stabilize and recover populations before extinctions occur (Kuussaari et al., 2009; Vellend et al., 2006). Restoring degraded habitats can increase target species' abundance and improve connectivity between fragmented habitats and populations.

That habitat restoration should lead to increased species’ abundance and persistence seems so self-evident that it can lead to unrealistic or undefined expectations and ineffective conservation outcomes. Implicit in many restoration projects is “The Field of Dreams Hypothesis” (Frick et al., 2014; Palmer et al., 2016), which assumes that: (1) habitat loss was the primary driver of the original population declines and, therefore, (2) there is a direct relationship between key habitat attributes (e.g., plant community composition and structure, wetland hydroperiod, disturbance regime, etc.) and the presence and abundance of a target species, and (3) species can and will naturally find and recolonize restored areas without additional management interventions (e.g., translocations). In practice, such relationships are more complex, and the effectiveness of habitat management actions are unlikely linear in time or space (Brown, 2023; Hilderbrand et al., 2005).

The implicit objectives of habitat restoration are to increase patch quality and decrease distance between patches. Colonization and population growth within restored habitats will lag following restoration depending on the species and the degree of isolation from potential source populations (Brown et al., 2023). In managed landscapes, rare species often persist as a network of patchy, remnant populations. The persistence of these networks, or metapopulations, depends on patch quality, patch distance, and the interaction of landscape structure with species-specific traits such as dispersal capacity (Brooks et al., 2002; Hanski & Ovaskainen, 2000; Tilman et al., 1994). For dispersal-limited species, restored habitat may remain uncolonized for a considerable time without intervention. Thus, preserving metapopulation processes in fragmented landscapes requires not only an understanding of both patch quality and distribution, but also of a species’ ability to recolonize after restoration (Bulman et al., 2007).

Another reason for the lag in time or failure of a species to recolonize restored habitat patches can be related to limitations in our ability to fully restore all the required elements for an area to support a species. Ecosystems that have evolved over millennia cannot easily be restored on a scale of years to decades (Hilderbrand et al., 2005; Hobbs & Norton, 1996). Therefore, restoration efforts may not meet the needs of some species over time scales relevant to managers. Historic land use, the complexity of managed landscapes, and the irreversible nature of some habitat loss further constrain species-specific outcomes (Yepsen et al., 2014).

Decisions about where and how to prioritize habitat restoration to meet management goals inherently involve uncertainty. Therefore, restoration efforts should intentionally incorporate clearly defined objectives and a monitoring and learning plan to adjust and improve management decisions over time (i.e., adaptive management; Lyons et al., 2008). By integrating monitoring and learning into the decision-making process, adaptive management provides a structured, iterative framework for conservation actions (Williams & Brown, 2018). Central to this framework is the “learning loop”: defining the problem, setting objectives, implementing actions, monitoring outcomes, and adjusting strategies accordingly (Canessa et al., 2019; Williams & Brown, 2012). Through the process of learning by doing, uncertainty is reduced over time, leading to better management decisions.

Wetlands, particularly small seasonally inundated geographically isolated wetlands, are critical habitats that have undergone extensive loss and degradation (Dahl, 2006). These wetlands provide valuable ecosystem services such as habitat provisioning, flood abatement, nutrient cycling, and carbon sequestration (Cohen et al., 2016; Lane et al., 2025; Leibowitz, 2003; Whigham, 1999). After a period of promoting wetland conversion for agriculture in the mid-1800’s (Swamp Land Acts, 1849, 1850, 1860), federal regulations shifted to protect remaining wetlands from loss (Clean Water Act, 33 U.S.C. §§ 1251–1387; Food Security Act of 1985, 16 U.S.C. §§ 3801–3865; National Environmental Policy Act of 1969, 42 U.S.C. §§ 4321–4370h), though degradation of wetlands often continued through neglect and poor management regimes (Dahl and Allord, 1996; Lang et al., 2024; McCauley et al., 2013). Wetlands are among the most vulnerable systems to pollution and species invasions and are prone to succession when disturbance regimes are altered. In 2023, the United States Supreme Court ruled in Sackett v. EPA (2023) to remove federal safeguards under the U.S. Clean Water Act from millions of small and isolated wetlands. The United States Department of Agriculture (USDA) and other agencies have initiated several conservation and mitigation programs, including the Farm Bill, the Wetlands Reserve Program, and The America the Beautiful Freshwater Challenge to incentivize the conservation and restoration of wetlands. The goal of these initiatives is to extend wetland hydroperiods and restore wetland biotic communities to pre-degradation conditions (NRCS, 2012). Restoration approaches often leverage remnant seedbanks to facilitate the recovery of wetland plant assemblages (Martin & Katherine Kirkman, 2009; Stonecypher et al., 2024), while hydrologic manipulations such as ditch plugging, basin reshaping, or drainage removal can increase water retention (Chimner et al., 2019; Sonnier et al., 2018). Such interventions can promote re-establishment of aquatic vegetation and reduce encroachment of xeric-adapted vegetation (Leeds et al., 2009).

Protection and restoration of wetlands is a high priority for amphibian conservation (IUCN SSC Amphibian Specialist Group, 2024; United States Environmental Protection Agency, 2021). Amphibians are the most imperiled vertebrate group globally (IUCN, 2023; Luedtke et al., 2023). Numerous studies have demonstrated that wetland restoration has the potential to increase amphibian occupancy and species richness (Burrow & Lance, 2022; Hossack et al., 2013; Klaus & Noss, 2016; Petranka et al., 2007; Walls et al., 2014). In the southeastern U.S, restoration of geographically isolated wetlands (GIWs) embedded within the longleaf pine (*Pinus palustris*) and wiregrass (*Aristida stricta*) ecosystem is a recently elevated priority for the conservation of a suite of amphibian species along with other wildlife, invertebrates, and plant species. The longleaf pine and wiregrass ecosystem that once dominated the southeastern landscape supports a high level of regional biodiversity (Kirkman et al., 1999) and GIWs account for a significant portion of that biodiversity (Gibbons et al., 2006; Liner et al., 2008; Smith et al., 2017). GIWs are naturally characterized by short to intermediate hydroperiods and frequent fires that maintain open canopies and diverse herbaceous plant communities (Gibbons et al., 2006; Gibbs, 2000; Kirkman et al., 2012; Leibowitz, 2003; Semlitsch & Bodie, 1998).

Upland restoration efforts have roughly doubled the amount of terrestrial longleaf pine habitat to about 6% since 2010 (NRCS, 2023) but restoration of the GIWs within those areas has lagged. Restoration of GIWs was identified in the 2015 and 2025 Georgia State Wildlife Action Plan (SWAP) where they ranked as high priority habitats for conservation in the Southeastern and Southern Coastal Plains Ecoregions. At least 13 species of amphibians associated with longleaf pine savannas breed exclusively in isolated wetlands (Smith et al., 2017) including five amphibian Species of Greatest Conservation Need (SGCN) identified in the 2025 Georgia SWAP. Such amphibians are considered specialists and are specifically adapted to the cycles of wetting and drying that often limit the establishment of predators like fish and dragonflies that prey on larvae (Burrow & Maerz, 2022; Liner et al., 2008). Klaus and Noss (2016) reported that some specialist and generalist amphibians were absent from GIWs where vegetation had shifted due to fire exclusion or other management, indicating the need for wetland vegetation restoration through tree and shrub removal/mulching and reintroduction of fire to establish conditions more suitable for amphibian occupancy. There is potentially high conservation value to restoring GIWs for amphibian species of conservation concern.

In addition to restoring wetlands, the intentional or unintentional (e.g., borrow pits) creation of artificial GIWs is also a potential action to provide habitat for amphibian species (Brand & Snodgrass, 2010; Brown et al., 2012; Petranka et al., 2003). These manmade water bodies tend to have extended hydroperiods and may serve as breeding sites for amphibians during dry years when natural wetlands fail to fill (Petranka et al., 2007). However, the long-term success of these created wetlands in providing habitat is still debated as longer hydroperiods can increase aquatic predator abundance including crayfish, dragonfly, or fishes (Julian et al., 2019; Petranka et al., 2007; Petranka & Holbrook, 2006) and disease prevalence (Petranka et al., 2007, Richter et al., 2013). While restored or manmade wetlands may provide suitable habitat for amphibians, recolonization of restored habitat will likely be dependent on the proximity of occupied source wetlands (Bartelt & Klaver, 2017; Gibbs, 2000; Lehtinen & Galatowitsch, 2001; Petranka & Holbrook, 2006).

In 2019 and 2022, the state of Georgia received Competitive State Wildlife Grants (U.S. Fish and Wildlife Service, 2025) to investigate the response of amphibians to wetland restoration and to investigate the response of amphibians and hydroperiod after plugging wetlands that were ditched for timber harvest. The Georgia Department of Natural Resources (Georgia DNR) initiated wetland restorations across three Wildlife Management Areas in South Georgia and partnered with the University of Georgia to begin the associated research for priority amphibian and plant SGCNs. Ideally, target wetland conditions for restoration actions should be evaluated to identify what approaches are most effective to achieve desired habitat conditions and target species responses. To determine the effects of wetland conditions on amphibians, we estimated occupancy rates for amphibian species as functions of wetland hydroperiod, canopy cover, and the distance to the nearest occupied wetland. We expected that occupancy of amphibians would generally increase with decreasing canopy cover percentage, increasing hydroperiod, and would be negatively correlated with the distance to the nearest occupied wetland.

Methods

Study Areas

The focal landscapes for this study were distributed across the southern Coastal Plain of Georgia within the historic range of the longleaf pine ecosystem (Figure 2.1). Between 2019 and 2024, we monitored 55 wetlands across four landscapes in Georgia: Alapaha River Wildlife Management Area (Alapaha) in Irwin County, Ceylon Wildlife Management Area and the adjacent Cabin Bluff conservation easement in Camden County (Ceylon), and the South section of Townsend Wildlife Management Area in McIntosh County (hereafter Townsend). The Jones Center at Ichauway (Ichauway) in Baker County, was added to the study in 2023 to supplement the number of study wetlands. The wetlands received a combination of restoration treatments, a single treatment, or no treatment at all. Of the 55 monitored wetlands, 23 experienced mechanical or chemical canopy thinning between 2019 and 2024 and 26 of the wetlands were burned with prescribed fire between 2019 and 2024. Four of the study wetlands were "constructed" borrow pits. The wetland conditions were considered "degraded" late succession vegetation states or various intermediate states up to target open canopy with emergent herbaceous vegetation. Sampling efforts were not equal among wetlands as some sites and wetlands were added as the study progressed. Following monitoring, 49 of the wetlands on three landscapes (Alapaha, Ceylon, Ichauway) were chosen for further analysis using an integrated occupancy model.

Alapaha River Wildlife Management Area

Alapaha is a 2,780-hectare property located in south central Georgia in Irwin County and managed by the Georgia Department of Natural Resources (Georgia DNR). This property was privately owned and managed for longleaf pine turpentine production and slash pine (*Pinus elliottii*) timber harvest until it was purchased by Georgia DNR in 2016 to create a Wildlife Management Area. The property in bordered by the Alapaha River and contains terrestrial uplands that include xeric sandhills and a large Gopher Tortoise (*Gopherus polyphemus*) population and other longleaf pine associates including remnant populations of Gopher Frogs and Striped Newts (*Notophthalmus perstriatus*), each known from only a single wetland in 2019 (Cork 2019). There are more than 55 isolated wetlands on the property. Some of these wetlands were historically ditched to reduce basin size and hydroperiod for silviculture, and some had historic fire breaks around the wetland margins. Due to the ditching and prolonged fire suppression, most of the property's wetlands were in first to secondary successional stages with heavy woody encroachment and dense shrub layers. intensive habitat restoration using canopy thinning and frequent prescribed fire have been ongoing since 2018 (Georgia Department of Natural Resources 2018). Terrestrial restoration has focused on thinning slash pine stands and replanting uplands in longleaf pine. In wetlands, management has focused on restoring wetland vegetation structure and hydrology for high priority amphibian species through canopy thinning and burning wetlands during the growing season. In 2022, three wetlands had ditches filled with the goal of restoring the natural hydroperiod (Bettcher, 2024). The results of Bettcher's research showed no detectable change in hydrology within the first year after ditch plugging. However, since 2023, it does appear that one of the plugged wetlands is now holding water longer (J.C. Maerz, unpublished data, 2025). It is noted that this change in hydrology is concurrent with apparent increased hydroperiods for many wetlands across the landscape associated with aggressive upland pine thinning.

Ceylon Wildlife Management Area and Cabin Bluff Easement

Ceylon is a 10,970 ha acre property located in coastal Southeast Georgia in Camden County. Celyon was purchased in 2021 and is managed by the Georgia DNR as a Wildlife Management Area. The Cabin Bluff Conservation Easement is an additional 1,295 ha property adjacent to Ceylon WMA. For the purposes of this study, the properties are considered a singular landscape. The landscape is a historic longleaf pine savanna, a high density of isolated wetlands, maritime forest, tidal river marsh, and salt marshes. Much of the longleaf pine was harvested after the Civil War, however approximately 1,619 ha of mature longleaf pine wiregrass habitat remained across the property. The landscape was previously managed as a hunting reserve with prescribed fire and low-impact, selective timber harvest, which maintained the soils and habitats in reasonably undisturbed condition. The landscape, particularly Ceylon, contains an abundant Gopher Tortoise population as well as remnant populations of Gopher Frogs and other priority species. The network of relatively intact isolated wetlands has provided key breeding habitat for priority amphibian species. Striped Newts have previously been found at one wetland on the property and may persist in very low numbers, though they have not been detected since 2008 (Farmer et al., 2017). Many of the wetlands have degraded over time from xeric woody succession. The density of terrestrial pine habitats surrounding the wetlands likely contributed to shortened hydroperiods that allowed sufficient time for shrub, hardwood, and pine intrusion into the wetland basins. Several wetlands on the property have been drained by ditching or by digging pits in the basins to concentrate water and reduce wetland surface area. There are several constructed borrow pits on the property that now function as isolated freshwater wetlands with long to relatively permanent hydroperiods. Ceylon represents the largest and highest quality coastal maritime and pine savanna habitat on public lands in Georgia. On the Cabin Bluff easement, six wetlands were selected as restoration sites for this study and were managed with canopy thinning, prescribed fire, or a combination. Several wetlands on Cabin Bluff are in degraded states with closed canopies, thick duff layers, and dense woody encroachment.

Townsend Wildlife Management Area

Townsend Wildlife Management Area is comprised of four contiguous tracts totaling in 12,950 ha of land on the north side of the Altamaha River in southeast Georgia in Long and McIntosh counties. The property was established as a Wildlife Management Area in 2006. The property includes xeric scrub-oak sandhills and bottomland hardwood swamps with many isolated wetlands scattered throughout the sandhills. The property was historically planted in Sand pine (*Pinus clausa*) and was replanted in Longleaf pine in 2017. The uplands contain a moderately abundant population of Gopher Tortoises. The property previously supported at least one population of Gopher Frogs known from a single record, though they have not been documented on the site since the 1990's. Georgia DNR partnered with the University of Georgia to restore upland and wetland habitat and has been releasing captive-reared Gopher Frogs on the property since 2018. The focal area for wetland restoration and monitoring was in the South Townsend section in the northeast corner of McIntosh County, Georgia. For this study, four wetlands were designated for restoration with all receiving repeated prescribed fire and two had canopy thinning in 2021. The wetlands were located in upland sandhills and had relatively short hydroperiods during most years (J. C. Maerz, unpublished data, 2024).

The Jones Center at Ichauway

Ichauway is a 11,700-ha private property located in Baker County in southwestern Georgia that was managed as a Northern bobwhite (*Colinus virginianus*) hunting preserve from the 1920s to early 1990s. The property has mature second growth longleaf pine and extensive native ground cover. The Longleaf pine savannas on Ichauway have been managed for over 80 years with frequent prescribed fire and single tree selection timber harvest and has preserved much of the original groundcover and limited soil disturbance. Ichauway is in the Dougherty Plain, a subregion of the Coastal Plain characterized by karst topography and limestone sinks, responsible for the more than 100 depressional, seasonal GIWs on the property. The matrix of longleaf pine uplands and GIWs has supported some of the most species-rich habitats in North America (Snodgrass et al., 2000), despite being surrounded by center-pivot agriculture. Ichauway contains many priority species including populations of Gopher tortoises, Gopher Frogs, and Eastern Tiger Salamanders. Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) and Striped Newts were last detected on Ichauway in 1997 and 2006 respectively and are believed to have been extirpated following a series of prolonged droughts (Farmer et al., 2017). This suggests that despite a large area of relatively well-managed upland habitat, conditions were insufficient to sustain populations of those amphibian species either due to extinction debt, a missing component of habitat, or other factor such as disease that went undetected. Most of the wetlands at Ichauway are considered to be in reference condition with open canopies, abundant emergent vegetation, and native groundcover maintained by frequent fire (1-2 year intervals). However, in some cases, e.g., where wildlife food plots or roads created fire shadows, Ichauway has implemented thinning and removal of woody encroachment in and around wetlands, followed by prescribed burns when wetlands are dry. Additionally, in 2018, Ichauway sustained damage from Hurricane Michael and lost approximately 16% of the trees across the site, effectively thinning the uplands site wide and likely impacting wetland hydrology (Jones et al., 2018; Rutledge et al., 2021).

Data Collection

We sampled 54 of the 55 monitored wetlands between 2018-2024 (Table 2.1), using Acoustic Recording Units (ARUs; SongMeter Minis and Micros, Wildlife Acoustics, Inc., Maynard, MA, USA). We placed ARUs on trees near the deepest part of each wetland, where water persisted the longest, to maximize the probability of recording anuran calls. We programmed the ARUs to record 5 minutes on the hour from 1800 h to 0200 h daily. We deployed ARUs from October-July when wetlands held water and removed them early if the wetland fully dried before July. We randomly selected two or three 5-minute call files from within 48 h of a rain event with > 0.25 mm of precipitation for analysis, which prior research showed is when detection of calling anuran species is maximal (Cork, 2019). Trained listeners identified all calls and assigned calling intensity scores using the North American Amphibian Monitoring Program (NAAMP) index (Weir & Mossman, 2005). For each recording, listeners gave each species a NAAMP score of 0-3 with 0 indicating no calling and 3 indicating a full chorus. We trained listeners using the United States Geological Survey’s NAAMP Frog Call Quiz and “test” call files until they consistently correctly detected and identified all potential anuran species in Georgia’s coastal plain. We spot-checked identifications throughout the training period and verified all files that needed identification confirmation.

From 2019-2024, we implemented wetland dipnet surveys in 52 of the 55 monitored wetlands. The dipnet surveys were comprised of two or three individuals sampling for a total of 1 person-hour (20-30 min per individual) each month at each wetland from November through July provided there was water in the wetland basin. For each observer, anuran and salamander species, life stage, and the total number captured were recorded. Observers also recorded metamorphosed amphibians observed or heard calling but not captured by dipnet.

We characterized wetland vegetation through field surveys and GIS mapping, except at Ceylon. Ceylon was added to the study in 2024 which was an abnormally high precipitation year. The wetland vegetation protocols used by Georgia DNR required the wetland basin to be dry or nearly dry, so vegetation sampling was not possible at these wetlands during the study. At all other sites, field surveys were performed in mid to late summer during "leaf-on" when wetland water levels are lowest and it is easiest to identify grasses and quantify canopy cover. The Georgia DNR Botany Team collected field data at Alapaha, Townsend, and Cabin Bluff in 2019 and 2022, and we collected field data on the study wetlands at Ichauway in 2023.

We followed Georgia DNR wetland restoration vegetation monitoring field protocol, which consisted of 6 50 m transects spaced at 60º intervals around the wetland's perimeter (Figure 2.2). We determined the wetland boundary at the transition from wetland to upland plant species or when available, we used existing wetland boundary layers; however, we found it necessary to re-delineate or update some wetland boundaries in GIS for Ceylon and Alapaha. Each transect began at the wetland boundary and extended toward the wetland centroid. Along transects, we classified vegetation into "zones" with a 2 m minimum length (Figure 2.3). At the midpoints and endpoints of each transect, we recorded canopy cover, litter depth, and tree basal area. The protocol defined canopy cover as all overhead vegetation that was visible when the densiometer was held at waist height, including understory trees and tall shrubs.

We also estimated vegetation cover types (below) at all study wetlands by photo interpretation of satellite imagery from 27 June 2024 during leaf-on, available through the ESRI World Imagery Wayback resource (ESRI 2024) in QGIS (2024). We divided cover classes into five categories: tree, shrub, herbaceous groundcover (graminoid and non-graminoid), sparse, and water. We calculated percentages of each class as a proportion of the total wetland area. We categorized the digitized canopy cover by percent tree cover, including tall shrubs large enough to cast detectable shadows.

Data Analysis

We used an integrated multi-season Bayesian community occupancy model (modified from Guzy et al. 2019 and Brown 2023) to estimate species-specific amphibian occupancy and detection probabilities and the influence of site characteristics on occupancy probability and richness as a function of site-specific covariates. To improve the estimates of detection, we incorporated multiple-methods and multiple-observer data within sampling events. We examined occupancy probabilities at the species-specific level, and we also used a grouping parameter where species were grouped by clade. We divided the 28 species into 6 groups where most species were binned at the genus level so that more well-detected species could inform related, but data-deficient species within the same group. For *Rana [Lithobates]*, we divided species into Aquarana (*R. clamitans*, *R. grylio, R. catesbeiana*), and the Leopard Frog (*R. sphenocephala*). We placed *Notophthalmus perstriatus*, *Pseudacris ornata*, and *Rana capito* based on similar ecological guilds. Prior to analysis, we decided to remove Townsend as a study landscape to improve model estimates since the wetlands rarely if ever filled for all study years. We also excluded one wetland at the Jones Center from the dataset because it did not hold water during the study period, and no amphibians were ever detected. We removed detections of *Anaxyrus fowleri* for the data analysis since the species was only detected one time at one wetland on Alapaha (Appendices 2.1–2.5).

We modeled true occupancy as $z_{s,j,w,t}$ such that if species *s* occupied site j at wetland w during year t, $z_{s,j,w,t}$ equaled one; otherwise $z_{s,j,w,t}$ equaled zero. We considered the latent occupancy state to be a Bernoulli random variable, $z_{s,j,w,t} \sim Bernoulli(\psi_{s,j,w,t}) * available_{s,(landscape(j)}$, where $\psi_{s,j,w,t}$ is the probability that species *s* occupies site *j* at wetland *w* in year *t* and $available_{s,(landscape(j)}$, is whether species *s* is available (in known species range) to be detected on each *landscape*. We modeled each year's latent occupancy independently because our dataset did not include enough years to reliably estimate colonization and extinction for a dynamic model. We modeled species-specific occupancy probability ($\psi_{s,j,w,t}$) as a linear-logit function of the model covariates:

$$logit(\psi_{s,j,w,t}) = \alpha 0_s + \alpha 1_s * CanopyCover_{j,w} + \alpha 2_s * \ Hydroperiod_{j,w} \ + \alpha 3_s * Distance_{w,j,s} + \ \alpha 4_s * Landscape_{s,landscape(j)}$$

We included a fixed effect of landscape on occupancy to account for variation across the three landscapes (Alapaha, Ceylon, and Ichauway). We defined the canopy cover covariate as the percent canopy cover of each wetland and site during our sampling year (2024) using QGIS. We defined a wetland hydroperiod covariate as the proportion of months of the year that each of the study wetlands held water (i.e., 1:12) in during the 2023-2024 sampling seasons (include months here). We calculated a covariate of the shortest distance to the nearest wetland occupied by the same species in meters. If there were no other detections on the landscape, we used the distance to the property boundary in meters. We centered and scaled each of the covariates.

We modeled species-specific detection probabilities as a linear-logit function of the model covariates within two observation processes. We conditioned both detection models on the latent occupancy state (z), such that detection was only possible if a species was present.

Dipnet detections:

$$Y.dip_{s,j,w,r,e,m,t} \sim Bernoulli\left(p.dip_{s,j,w,r,e,m,t} * z.dip_{s,j,w,t} * effort.dip_{s,j,w,r,e,m,t} * available_{s,(landscape(j))}\right)$$

Where:

$$logit\left(p.dip_{s,j,w,e,r,m,t}\right) = \beta 0.dip_s + \beta 1_j + \beta.Month.dip_{s,m} + \beta.Year.dip_{s,t}$$

Acoustic detections (ARUs):

$$Y.call_{s,j,w,r,e,m,t} \sim Bernoulli\left(p.call_{s,j,w,r,e,m,t} * z.call_{s,j,w,t} * effort.call_{s,j,w,r,e,m,t} * available_{s,(landscape(j))}\right)$$

Where:

$$logit\left(p.call_{s,j,w,e,r,m,t}\right) = \beta 0.call_s + \beta 1_j + \beta.Month.call_{s,m} + \beta.Year.call_{s,t}$$

We modeled the true occupancy state separately for ARU and dipnet data as $z.call_{s,j,w,t}$ and $z.dip_{s,j,w,t}$ such that if species *s* occupied site *j* at wetland *w* during year *t* $z.call_{s,j,w,t}$ and $z.dip_{s,j,w,t}$ equaled one; otherwise $z.call_{s,j,w,t}$ and $z.dip_{s,j,w,t}$ equaled zero. We constructed effort arrays to capture variation in sampling effort across species, sites, wetlands, replicates, events, months, and years. We converted multi-observer data into replicate trials within each sampling event, providing replication to improve detection estimates. We included month as a random effect and year as a fixed effect on detection to represent biologically meaningful variation. Month effects reflected variation in seasonal breeding phenology between species, and year effects accounted for annual precipitation patterns that influence species-specific breeding (Jensen et al. 2008). We estimated site richness by identifying species whose latent occupancy state was positive ($z = 1$) for at least one wetland and one year within each site and then summing the number of such species per site. The model used an integrated framework to specify separate detection sub-models while linking them to a shared latent occupancy state.

We fit the model using JAGS (Plummer 2023) in R v4.5.0 (R Core Team 2018) with the jagsUI package (Kellner 2016). We implemented the model in a Bayesian framework and used Markov Chain Monte Carlo (MCMC) sampling to generate posterior samples. We ran three parallel chains of 15,000 iterations each, discarded the first 7,500 iterations as burn-in and thinned the remainer by a factor of 10. This produced 2,250 posterior samples per parameter. We summarized posterior distributions for each model parameter as means and 95% Bayesian credible intervals. We used the GelmanRubin statistic and a visual inspection of MCMC trace plots from the model outputs to assess model convergence.

Results

We made 4,253 independent detections of 28 amphibian species via dipnet sampling and 15,016 independent detections of 20 anuran species detected via ARU (Table 2.1). Across all surveys and methods, we detected 6 salamander species and 22 anuran species (Table 2.2). Model posterior visual inspection and the Gelman-Rubin statistic (Gelman and Rubin 1992) indicated partial model convergence. Most species-specific covariate effects had 95% credible intervals that overlapped zero, indicating weak or inconsistent support for directional relationships between occupancy and covariates. Visual inspection of the chains showed adequate model convergence and mixing in 1134 parameters out of 1268 model parameters (89%), with the remaining exhibiting some degree of non-convergence (Appendix 2.6). Six percent of parameters (n = 87) had R-hat values between 1.00 and 1.02; four percent (n = 47) had R-hat values between 1.2 and 1.046; none exceeded 1.046 (Appendix 2.6). Although these values suggest that the degree of non-convergence was limited, poor mixing reduces confidence in effect estimates and introduces uncertainty regarding the magnitude and direction of model outputs. Therefore, any inferences or conclusions drawn from these results must be qualified and considered provisional until resolved in future analysis.

In our study, two species, the Southern Cricket Frog (*Acris gryllus*) and Southern Leopard Frog (*Rana sphenocephala*) were detected at 54 of the 55 monitored wetlands and all 49 study wetlands (naïve occupancy = 0.98; Table 2.2). Eighteen additional species of anurans were detected at 14-53 wetlands (naïve occupancy rates = 0.26-0.98; Table 2.2). Some moderately common species not detected in all landscapes were not detected in all landscapes. The Eastern Tiger Salamander, detected at Alapaha and Ichauway in 21 wetlands (naïve occupancy rate = 0.39); the Narrowmouth Toad (*Gastrophryne carolinensis*) was detected at 29 wetlands (naïve occupancy rate = 0.54), in all landscapes; and the Green Frog (*Rana clamitans*) was detected at 39 wetlands (naïve occupancy rate = 0.72) but not detected on Ichauway (Table 2.2). Three species were detected at 7-13 wetlands, including the Southeastern Dwarf Salamander (*Eurycea quadridigitata*) detected at Alapaha, Ichauway, the Eastern Newt (*Notophthalmus viridescens*) detected on all landscapes except Townsend, and the Mole salamander (*Ambystoma talpoideum*) was detected only at Alapaha and Ichauway (naïve occupancy rate = (0.13-0.37) (Table 2.2). Bird-Voiced Treefrog (*Hyla avivoca*) was only detected in 2019 and 2021 at a single wetland on Alapaha (Table 2.2). Dwarf Sirens (*Pseudobranchus striatus*) were detected at two wetlands on Ichauway, and the Striped Newt was detected at one wetland on Alapaha (naïve occupancy rate = (0.02 -0.04; Table 2.2). The mean estimated amphibian species richness at each site was 25 at Alapaha, 21 (19-23) at Cabin Bluff, 23 (20-24) at Ceylon, 25 (23-26) at Ichauway (Table 2.3).

Group-specific responses to site conditions varied widely across taxa (Table 2.3; Figure 2.4). Most estimates had high uncertainty with 95% credible intervals overlapping zero, indicating weak or inconsistent evidence for relationships between occupancy and site covariates at the group level (Table 2.3). The parameters at the group levels that showed higher posterior support (greater than 0.80) included canopy cover and distance to nearest occupied wetland for *Anaxyrus* and hydroperiod for *Pseudacris* (Table 2.3). For *Anaxyrus* the model predicted that occupancy tended to decrease with increasing canopy cover (mean = -0.66, 95% CI = –2.13 to 0.81, Bayesian p-value = 0.88) and distance to the nearest occupied wetland (mean = –0.602, 95% CI = –1.96 to 0.96, Bayesian p-value = 0.84) (Table 2.3). For *Pseudacris* the model predicted that occupancy decreased with increasing hydroperiod (mean = -0.79, 95% CI = –2.29 to 0.55, Bayesian p-value = 0.89) (Table 2.3). All groups had mean estimates centered near zero with wide credible intervals and low Bayesian p-values for most parameters, indicating little support for group level relationships between occupancy and site covariates, though some Bayesian p-values suggested directionality (*Pseudacris* occupancy increasing with increasing canopy cover, Bayesian p-value = 0.88; *Ambystoma* decreasing with distance to nearest occupied wetland, Bayesian p-value = 0.79; Table 2.3; Figure 2.4).

Species-specific responses to site covariates were also highly variable across taxa (Table 2.4: Figure 2.5). Several species exhibited high posterior sign probabilities (> 0.95) or credible intervals that excluded zero, suggesting directional effects on occupancy (Table 2.3). Strong negative associations with canopy cover were observed for *Anaxyrus quercicus*, *Notophthalmus perstriatus*, and *Scaphiopus holbrookii* (Table 2.4; Figure 2.5; Figure 2.7). *Ambystoma tigrinum*, *Hyla chrysoscelis*, *Notophthalmus viridescens*, and *Pseudacris nigrita* all exhibited strong negative associations with increasing hydroperiod (Table 2.4; Figure 2.5; Figure 2.7). Only *Eurycea quadridigitata* had strong posterior support for a negative association with distance to occupied wetlands. Several species showed moderately high posterior support (>0.90) for parameters (Table 2.4). *Notophthalmus viridescens* had moderately high posterior support for a negative relationship with canopy cover, and *Pseudacris ocularis* and *Rana grylio* occupancy were positively associated with canopy cover (Table 2.4; Figure 2.5; Figure 2.7). *Pseudacris feriarum* had moderately high support for a negative relationship with hydroperiod and *Ambystoma tigrinum* and *Anaxyrus quercicus* occupancy were both negatively associated with increasing distance from occupied wetlands (Table 2.4; Figure 2.5; Figure 2.7).

For the four species of conservation concern, relationships to site conditions varied in both direction and strength (Table 2.4; Figure 2.9). *Rana capito* showed no strong evidence for effects of any wetland conditions on occupancy, as 95% credible intervals for all covariates widely overlapped zero and all Bayesian p-values were less than 0.65 (Table 2.4). For *Pseudacris ornata* there appeared to be moderate evidence for a negative relationship between occupancy and hydroperiod (mean = –0.53, 95% CI = –1.59 to –0.55, p = 0.84; Table 2.4; Figure 2.7; Figure 2.9). For *Ambystoma tigrinum*, there was strong support for negative relationships with hydroperiod (mean = –1.44, 95% CI = –2.58 to –0.474, p = 0.99), and distance to occupied wetlands (mean = –1.29, 95% CI = –3.39 to –0.49, p = 0.93), indicating preference for more ephemeral wetlands and the potential importance of nearby source wetland or adjacent populations (Table 2.4; Figure 2.7; Figure 2.8; Figure 2.9). *Notophthalmus perstriatus* showed a negative associations with both canopy cover (mean = –1.17, 95% CI = –3.06 to 0.09, p= 0.96) and hydroperiod (mean = –0.696, 95% CI = –2.33 to 0.48, p= 0.85), suggesting greatest occupancy in more ephemeral wetlands that were maintained in open canopy (Table 2.4; Figure 2.6; Figure 2.7; Figure 2.9).

The effect of landscape on occupancy probability varied among taxa (Figure 2.10). For example, *Hyla squirella* showed little variation among landscapes, while *Pseudacris ocularis* exhibited positive effects for all landscapes except Ichauway (Figure 2.10). *Acris gryllus* showed consistently positive landscape effects across all landscapes (Figure 2.10). Among the four priority species, *Rana capito* had positive landscape effects only at Ichauway and negative effects at Alapaha and Ceylon (Figure 2.10; Figure 2.0.1). *Notophthalmus perstriatus* was detected at a single wetland on Alapaha and had uniformly negative landscape effects across all study areas except Alapaha (Figure 2.10; Figure 2.0.1). *Pseudacris ornata* showed positive landscape effects at Alapaha and Ichauway and negative effects at Ceylon, while *Ambystoma tigrinum* showed positive effects only at Ichauway (Figure 2.10; Figure 2.0.1).

Canopy cover values were well distributed across the 55 monitored wetlands (Figure 2.0.2). However, when canopy cover was grouped by site, a clear landscape bias emerged. Wetlands at Ichauway consistently had lower canopy cover than those at Alapaha or Ceylon (Figure 2.0.3). The eight wetlands with the highest canopy cover occurred exclusively at Alapaha or Ceylon, whereas six of the seven lowest canopy cover wetlands were located on Ichauway (Figure 2.0.2; Figure 2.0.3).

Detection probability varied among species, survey method, and month. Peak detection of amphibian species in dipnet samples occurred from February through June (Figure 2.0.4). The *Pseudacris* had highest detection in late winter and early spring (January-April), followed by rapid declines later in the season. Species associated with longer hydroperiods, including *Rana catesbeiana*, *Rana clamitans*, and *Rana grylio*, maintained moderate to high detectability into mid and late summer (Babbitt et al., 2003; Babbitt & Tanner, 2000; Bury and Whelan 1985). *Ambystoma tigrinum* showed higher early-season dipnet detection (December–April), and *Notophthalmus perstriatus* had positive detection probability in winter (October–December) and late-spring (May–June) (Figure 2.0.4). Across most species, dipnet detection probability was negative near zero from August through December (Figure 2.0.4). Dipnet captures fluctuated among species, frequently switching direction between years, with the highest mean detection estimates occurring in 2024 when 22 species showed positive year effects (Figure 2.0.4). Detection probabilities from call surveys were comparatively stable, with monthly effects near zero and narrow credible intervals, and yearly effects generally small or negative (Figure 2.0.4).

Discussion

Our objective was to evaluate current amphibian occupancy relative to wetland conditions on four landscapes in the Southeastern coastal plain. Wetland restoration has been ongoing or recently initiated in each landscape commensurate with upland habitat restoration and management, but differences in the time since restoration actions including very recent actions on several landscapes precluded direct evaluation of restoration effects on amphibians. Therefore, we used current conditions among wetlands within and among landscapes to understand how wetland conditions currently shape the distribution of amphibians as a proxy for expected effects of restoration actions over the longer term. Because several parameters exhibited incomplete chain mixing, the inferences drawn here should be treated as provisional until further analyses resolve remaining uncertainty. Our current findings suggest that wetland conditions (canopy cover, hydroperiod, and distance to nearest occupied wetland) had variable but generally directional effects on amphibian occupancy. Generally, occupancy declined with increasing canopy cover, shorter hydroperiod, or increasing distance to other occupied wetlands. Which variables were correlated with occupancy varied among species and there were species and groups of species for which these generalities were reversed. We conclude that certain restoration actions to reduce canopy cover (e.g., tree and shrub removal or prescribed fire) and increase hydroperiod (reducing terrestrial and wetland tree biomass or filling ditches or pits constructed to drain wetlands) could lead to increased occupancy of priority species and overall amphibian richness; however, we caution that responses may be constrained by the current status of species on landscapes that are legacies of past landscape conditions. Our results indicate a high level of uncertainty about the influence of canopy cover and hydroperiod on current occupancy rates. We extend that high uncertainty to potential effects of wetland restoration. Without additional actions such as translocations or population supplementation, it is possible that responses to restoration actions may be delayed or fail to achieve desired outcomes.

Species-specific responses were highly variabile, likely reflecting diversity among amphibian life histories, dispersal capabilities, and habitat specialization. Salamanders (*Ambystoma, Eurycea, Notophthalmus*) showed negative effects of increasing hydroperiod, consistent with a other studies demonstrating these species are most associated with ephemeral wetlands where predation risk from fish is low (Semlitsch, 1980, 1987, 2000; Table 2.4 Figure 2.7). In our analysis, this association with hydroperiod included *Pseudobranchus striatus*;

however, this contradicts what is reported for the species' natural history. *Pseudobranchus* known life history as an obligate-paedomorph and its dependence on semi-permanent to permanent wetlands (Jensen et al. 2008). It is possible that the estimated relationship indicates that *Pseudobranchus striatus* occupancy is not directly responding to more ephemeral wetlands but is responding positively to shorter hydroperiods which facilitate more frequent fire in the wetland and maintain open canopies. We are cautious about our inferences because *P. striatus* was only detected at two wetlands within a single landscape where burn intervals have averaged 1-2 years for more than 50 years.

One species of conservation concern, *Notophthalmus perstriatus*, showed evidence of higher occupancy probability in wetlands with lower canopy cover and shorter hydroperiods, potentially reflecting the benefits of more open, fire maintained ephemeral habitats that promote herbaceous vegetation. However, we caution that these relationships had high uncertainty, and the species was only detected in a single wetland within a single landscape. Some of this pattern may be attributed to grouping effects with other species of conservation concern (*Rana capito*, *Pseudacris ornata*), which while known to breed in the same or similar wetlands, may have life history traits that allow them to tolerate a wider range of wetland conditions and persist in landscapes where *Notophthalmus perstriatus* have been extirpated.

The inclusion of group-level effects in the occupancy model likely enhanced some inference by allowing parameter estimates to draw information from closely related taxa, improving precision for data-limited species. Partial-pooling and hierarchical structure can be particularly valuable in amphibian community models where detection probabilities are low and sample sizes vary among species (Guzy et al., 2019; Kéry & Royle, 2016). However, pooling at the genus level can also mask meaningful ecological differences when taxa within groups differ in habitat use or life history, despite being closely related. For instance, while *Hyla avivoca* and *Hyla squirella* are similar in morphology and moderately related taxonomically (both are members of sister clades within the Hylidae (Hua et al., 2009)), they differ in breeding habitat specialization and apparent sensitivity to hydrology. *Hyla squirella* occurs commonly beyond the southeastern coastal plains and is found breeding in a variety of water bodies embedded within a wide range of terrestrial habitats including agricultural and urban systems. Within our three study landscapes, *H. squirella* was detected breeding in 39 wetlands while *H. avivoca* was rare and only detected twice in two different years at the same wetland (Table 2.2). Thus, while group-level pooling can improve model stability, it can also moderate important ecological differences among taxonomically related species. Future modeling efforts may benefit from grouping by ecological guild rather than taxonomy, but this may not be possible for all species in all ecological communities (Dorazio & Connor, 2014).

We caution that the absence of strong model-derived effects does not necessarily imply ecological insensitivity, but rather reflects statistical limitations associated with high occupancy and low variation in presence of some species (e.g., *Acris gryllus*) (Cressie et al., 2009), or high bias in the wetland conditions among landscapes. Rarely detected species, like *Pseudobranchus striatus,* had few detections, leading to broad posterior distributions. These patterns illustrate the challenges of modeling species-specific responses and the value of using Hierarchical Bayesian modeling approaches to stabilize estimates while acknowledging uncertainty. Continued sampling and additional data, particularly for species of conservation concern or rare species, will be necessary to refine estimates and capture longer-term response trends for these species.

Our results suggest that landscape legacies have a strong effect on wetland occupancy by amphibians that are not easily altered in the short term by management actions (Figure 2.10;

Figure 2.0.1). Differences among landscape size, land use, and management likely contribute to landscape-level variation. For example, Ceylon and Ichauway are much larger landscapes than Alapaha. Ichauway has been maintained in a largely desirable ecological state for more than fifty years (Boring 2001), while Alapaha and Ceylon very recently came under state management. These landscape differences, coupled with biases in the distributions of the spatial or temporal extent of management actions, and current conditions (e.g., wetland canopy closure) may overwhelm detectable short-term effects of wetland management. It is likely that the most immediate effects of management would be detected in demographic responses of relatively common species (e.g., *Rana sphenocephala*) that are too saturated on the landscape for occupancy studies to detect effects. Occupancy of less common and rare species likely takes longer to respond and detect through monitoring.

The effect of landscape on patterns of occupancy was particularly acute for our focal priority amphibian species. We did not detect *Ambystoma tigrinum* in one of our three landscapes. Ceylon is outside the known range for *Ambystoma tigrinum* in Georgia, so it is likely the species is not naturally present on that landscape. *Pseudacris ornata* was present and detected in all three landscapes but was common and abundant within two landscapes and rare in the other one landscape. Recent evidence shows that 33% of historic *Pseudacris ornata* populations have likely been extirpated, with most of those declines occurring in South Georgia, north Florida, and south Alabama (Koen et al., 2025). Despite previous research suggesting that vegetation management should benefit *Pseudacris ornata* (Burrow & Maerz, 2021), wetland occupancy at Ichauway and Alapaha is already saturated and unlikely to increase in response to management actions. Detecting management responses for this species may therefore require using measures of abundance or demographic rates. In contrast, if other factors unrelated to habitat conditions limit *Pseudacris ornata* or *Ambystoma tigrinum* populations at Ceylon, habitat management actions alone may not affect the occupancy rates of those species in those landscapes.

Although *Notophthalmus perstriatus* and *Rana capito* historically occurred in all three landscapes, limited detections suggest that restoration alone is likely insufficient for population recovery without additional interventions. In our study, *Notophthalmus perstriatus* was detected in only one wetland in one landscape since 2019. The species was last detected in the two other focal landscapes in 2006 and 2008 (Farmer et al. 2017). *Rana capito* was detected on all three focal landscapes but was abundant at multiple wetlands only at Ichauway, suggesting population status at each landscape strongly shapes the time it may take for species to respond to management. The rarity and isolation of *Rana capito* and *Notophthalmus perstriatus* populations suggest that habitat management alone may not be sufficient for species recovery and population supplementation via translocation or captive rearing will be needed in combination with restoration to improve relic or extirpated populations (Armstrong & Seddon, 2008; Ewen & Armstrong, 2007; Martin et al., 2025). Without further management intervention, there may be substantial time between management and detectable population effects.

The distance to the nearest occupied wetland provides an additional indicator of the importance of landscape level conditions and the potential need for supplemental actions. For several species (*Ambystoma tigrinum*, *Anaxyrus quercicus*, *Eurycea quadridigitata*) with high posterior support (Bayesian p-value > 0.90) for a negative relationship between occupancy and distance, consistent with limited dispersal capacities and low natural recolonization. In landscapes where these amphibians are experiencing declines, prioritizing improved connectivity and consideration of assisted colonization or translocation may be necessary to improve species occupancy in relevant management time scales.

Our ability to isolate the effect of individual restoration actions was constrained by inconsistencies in monitoring effort, uneven implementation of restoration actions, and a relatively small sample size of wetlands compared to the complexity of the questions addressed. Because restoration was often applied opportunistically and at varying intensities, we cannot attribute changes in amphibian occupancy to specific treatments. We therefore relied on measures of canopy cover and hydroperiod as indicators of habitat conditions expected to increase amphibian occupancy. In the Southeastern Coastal Plain, canopy thinning and prescribed fire are the primary techniques to produce and maintain open-canopy wetland conditions. These actions influence wetlands through similar ecological pathways by increasing light availability and promoting favorable hydrology, which our results suggest are associated with higher amphibian occupancy. Thus, achieving the desired habitat state may be more consequential than the specific method used to reach it.

Ditch plugging is another management action intended to restore wetland hydrology. Three wetlands in this study had ditches plugged, all in the same recent year and within the same landscape. Previous work by Bettcher (2024) at the same three wetlands found little to no hydrologic response during the initial year following hydrologic plugging. It is unclear whether the limited ditch plugging that has occurred among our study landscapes has produced measurable short-term benefits to amphibian occupancy. The temporal scale of both our study and Bettcher's work may be insufficient to detect longer-term ecological responses, as hydrologic recovery from basin erosion and prolonged drainage likely occurs over a scale of decades (Blann et al., 2009). Therefore, it remains to be seen whether ditch plugging will yield longer-term, sustained improvements to amphibian occupancy. In our study, plugged wetlands showed neutral to non-negative effects on species' occupancy, suggesting no evidence of short-term harm. Hydrologic restoration through ditch plugging may still represent an important long-term management investment for amphibian communities in ditched landscapes.

Our analysis did not account for concurrent upland management at some landscapes that likely interacted with wetland restoration to influence amphibian occupancy. Other studies have established a clear linkage between upland pine forest basal area and wetland hydrology and likely the capacity to support amphibian breeding as well (Golladay et al., 2021; Jones et al., 2018). Ceylon and Alapaha underwent substantial upland thinning between 2017 and 2024 that continues today and Ichauway experienced significant natural upland thinning from Hurricane Michael in 2018 (Rutledge et al., 2021). Upland thinning or loss of forest cover from hurricanes may be disturbances that affect near-term patterns of amphibian occupancy or abundance as well as longer-term changes in amphibian occupancy or abundance depending on how upland conditions are maintained post disturbance (Jones et al., 2018).

Our findings are consistent with recent research by Brown (2023), that suggests wildlife can exhibit highly variable, species-specific responses with potentially pronounced time lags following restoration actions. Lags may result from incomplete or lagging changes in habitat conditions and spatial conditions within landscapes that determine colonization rates of restored habitats. Our findings suggest that restoration actions focused on establishing or maintaining open canopies, particularly prescribed burning and canopy thinning, may have highly uncertain effects that are either beneficial or benign for amphibian occupancy in the near term. We found little evidence that restoration actions that decrease canopy cover would have negative effects on amphibian community occupancy. Therefore, the continuation of restoration efforts aimed at reestablishing open-canopy pine conditions and reconnecting isolated wetlands to improve the resilience of amphibian populations remains warranted at this time. However, our results highlight the need for quantitative metrics of restoration (e.g., basal area removed, percent canopy cover thinned, confirmation and extent of wetland basin burned) and long-term monitoring to capture delayed amphibian community responses, especially for rare taxa or those with episodic recruitment, so that any negative emerging effects can be identified or additional management actions can be incorporated to improve decisions and better meet management long-term objectives. For example, population supplementation is likely to be required in conjunction with habitat management to recover priority amphibian populations in landscapes where populations are currently small or recently extirpated. Without such actions, habitat restoration alone may not yield stable populations within a reasonable timeframe.

We advocate for the formal adoption of an adaptive management framework for ongoing restoration projects by land and wildlife management agencies or organizations to improve learning from ongoing management and improve future decision making. Given the natural variability of amphibian breeding dynamics, strategic and rigorous monitoring will remain essential in the near term but will ultimately enhance the effectiveness and efficiency of restoration outcomes. Our study illustrates the potential for such an adaptive management program to link management actions to measurable learning outcomes provided there is adequate design and execution of management actions and subsequent monitoring (Williams & Brown, 2018). Our study demonstrates the challenges of implementing restoration and subsequent monitoring at a temporal and spatial scale that will inform efforts to adaptively manage for amphibian species. Ongoing and future restoration efforts clearly serve as actions and opportunities to inform future management decisions. However, this process depends on the thoughtful planning and distribution of actions, consistent monitoring across relevant temporal and spatial scales, and the use of robust models that can account for imperfect detection and incorporate multiple monitoring methods. Without well-replicated restoration treatments and robust monitoring and analyses, the inherent bias and variability within and among landscapes are likely to make it difficult to evaluate whether management actions are having desired effects. For rare and threatened species, high uncertainty and delays in learning whether actions are working can prove particularly costly with the loss of few remaining populations. Restoration efforts must incorporate and commit resources to clearly defined learning components prior to implementation, emphasizing hypothesis-driven management, standardized protocols, multiple methods, and iterative evaluation to ensure actions advance conservation outcomes and ecological understanding (Williams & Brown, 2012).

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Tables

Table 2.1. Summary of amphibian detections by wetland across four landscapes in Georgia, USA. Values are the total number of species and cumulative observations recorded from dipnet and acoustic surveys from 2019 to 2024.

Landscape	Wetland ID	Total Species	Total Observations (2019 -2024)
Alapaha River WMA	10	19	661
Alapaha River WMA	15	18	817
Alapaha River WMA	18	23	873
Alapaha River WMA	20	21	357
Alapaha River WMA	23	17	531
Alapaha River WMA	29	19	568
Alapaha River WMA	3	22	1007
Alapaha River WMA	30	22	681
Alapaha River WMA	31	21	652
Alapaha River WMA	32	22	471
Alapaha River WMA	34	21	580
Alapaha River WMA	39	19	628
Alapaha River WMA	4	17	315
Alapaha River WMA	41	20	635
Alapaha River WMA	42	20	688
Alapaha River WMA	43	21	721
Alapaha River WMA	8	20	724
Ceylon WMA/Cabin Bluff	170	15	187
Ceylon WMA/Cabin Bluff	179	16	167
Ceylon WMA/Cabin Bluff	183	7	131
Ceylon WMA/Cabin Bluff	184	9	147
Ceylon WMA/Cabin Bluff	189	9	176
Ceylon WMA/Cabin Bluff	290	8	49
Ceylon WMA/Cabin Bluff	109	10	108
Ceylon WMA/Cabin Bluff	109B	14	160
Ceylon WMA/Cabin Bluff	127	16	216
Ceylon WMA/Cabin Bluff	22	9	258
Ceylon WMA/Cabin Bluff	37	11	297
Ceylon WMA/Cabin Bluff	41	12	166
Ceylon WMA/Cabin Bluff	41B	13	235

Landscape	Wetland ID	Total Species	Total Observations (2019 -2024)
Ceylon WMA/Cabin Bluff	54	13	287
Ceylon WMA/Cabin Bluff	55	14	165
Ceylon WMA/Cabin Bluff	59	17	394
Ceylon WMA/Cabin Bluff	60	6	7
Ceylon WMA/Cabin Bluff	62	13	200
Ceylon WMA/Cabin Bluff	69	13	264
Ceylon WMA/Cabin Bluff	69B	6	10
Jones Center Ichauway	15	16	269
Jones Center Ichauway	21	14	174
Jones Center Ichauway	37	11	226
Jones Center Ichauway	41	14	326
Jones Center Ichauway	42	19	397
Jones Center Ichauway	46	17	526
Jones Center Ichauway	49	13	214
Jones Center Ichauway	50	18	204
Jones Center Ichauway	51	15	202
Jones Center Ichauway	53	15	150
Jones Center Ichauway	55	22	568
Jones Center Ichauway	40	13	274
Townsend WMA	Cutgrass	13	556
Townsend WMA	Deadwood	7	106
Townsend WMA	Milfoil	8	30
Townsend WMA	Plum Orchard	16	280
Townsend WMA	Snot Bonnet	11	236

Table 2.1. Summary of amphibian species detections by method across four landscapes in Georgia, USA. Values are the total number of detections in dipnet surveys, acoustic recording units (ARUs), cumulative observations recorded, and total number wetlands occupied from 2019 to 2024.

Species	Dipnet Observations	ARU Observations	Total Observations	Number of Wetlands
Acris gryllus	774	2554	3328	54
Ambystoma talpoideum	12	0	12	7
Ambystoma tigrinum	93	0	93	21
Anaxyrus fowleri	0	1	1	1
Anaxyrus terrestris	34	168	202	40
Anaxyrus quercicus	54	206	260	35
Eurycea quadridigitata	76	0	76	20
Gastrophryne carolinensis	58	363	421	39
Hyla avivoca	2	0	2	1
Hyla chrysoscelis	60	116	176	30
Hyla cinerea	28	481	509	40
Hyla femoralis	351	962	1313	53
Hyla gratiosa	252	467	719	44
Hyla squirella	38	186	224	39
Notophthalmus perstriatus	19	0	19	1
Notophthalmus viridescens	29	0	29	14
Pseudacris crucifer	186	1723	1909	50
Pseudacris feriarum	25	0	25	14
Pseudacris nigrita	227	878	1105	38
Pseudacris ocularis	481	2423	2904	45
Pseudacris ornata	330	667	997	34
Pseudobranchus striatus	6	0	6	2
Rana capito	28	219	247	20
Rana catesbeiana	98	428	526	33
Rana clamitans	87	412	499	39
Rana grylio	84	263	347	26
Rana sphenocephala	764	2446	3210	54

Table 2.3. Summary of predicted mean amphibian species richness at each site from 2019-2024. Mean Site richness represents the estimated mean amphibian species richness. Lower CI and upper CI represent the 95% Bayesian credible interval for each site's predicted species richness.

Site	Mean Site Richness	Lower CI	Upper CI
Alapaha River WMA	25.00	25	25
Cabin Bluff	21.70	19	24
Ceylon WMA	22.40	20	24
Jones Center at Ichauway	24.53	22	26

Table 2.3. Posterior summaries of species-specific estimates on occupancy probability from an integrated Bayesian occupancy model. Values represent posterior means, 95% credible intervals, and Bayesian p-values (the proportion of posterior simulations consistent in sign with the mean estimate). Estimates in bold indicate parameters for which the Bayesian p-value > 0.80.

Group	Group-specific parameter	Mean	95% CI		Bayesian p-values
Ambystoma	Canopy Cover	-0.190	-2.021	1.558	0.597
	Hydroperiod	-0.073	-2.123	2.277	0.552
	Distance	-0.696	-2.645	1.301	0.795
Anaxyrus	**Canopy Cover**	**-0.656**	**-2.126**	**0.810**	**0.876**
	Hydroperiod	-0.067	-1.565	1.461	0.536
	Distance	**-0.602**	**-1.964**	**0.960**	**0.838**
Aquarana	Canopy Cover	0.094	-1.401	1.672	0.558
	Hydroperiod	0.009	-1.126	1.170	0.503
	Distance	-0.449	-2.034	0.900	0.755
Hyla	Canopy Cover	-0.245	-1.178	0.643	0.736
	Hydroperiod	-0.200	-1.048	0.649	0.692
	Distance	0.048	-0.636	0.803	0.562
Pseudacris	Canopy Cover	0.480	-0.840	1.924	0.791
	Hydroperiod	**-0.785**	**-2.291**	**0.547**	**0.888**
	Distance	-0.205	-1.827	1.314	0.612
SGCNs	Canopy Cover	-0.457	-2.020	1.079	0.767
	Hydroperiod	-0.568	-2.242	1.036	0.788
	Distance	-0.446	-1.788	1.058	0.780

Table 2.4. Posterior summaries of species-specific estimates on occupancy probability from an integrated Bayesian occupancy model. Values represent posterior means, 95% credible intervals, and Bayesian p-values (the proportion of posterior simulations consistent in sign with the mean estimate). Estimates in bold indicate parameters for which the Bayesian p-value > 0.80.

Species	Species-specific parameter	Mean	95% CI		Bayesian p-values
Acris gryllus	Canopy Cover	0.143	-2.263	2.144	0.590
	Hydroperiod	0.153	-1.820	1.822	0.587
	Distance	0.561	-1.175	2.588	0.714
Ambystoma talpoideum	Canopy Cover	-0.463	-2.556	1.173	0.691
	Hydroperiod	**1.333**	**-1.302**	**4.568**	**0.810**
	Distance	**-0.640**	**-1.723**	**0.407**	**0.891**
Ambystoma tigrinum	Canopy Cover	-0.072	-1.061	0.829	0.557
	Hydroperiod	**-1.443**	**-2.578**	**-0.474**	**0.996**
	Distance	**-1.294**	**-3.389**	**0.490**	**0.932**
Anaxyrus quercicus	**Canopy Cover**	**-0.839**	**-1.927**	**0.042**	**0.968**
	Hydroperiod	**0.669**	**-0.424**	**1.970**	**0.884**
	Distance	**-0.918**	**-2.418**	**0.327**	**0.931**
Anaxyrus terrestris	**Canopy Cover**	**-1.001**	**-3.495**	**0.698**	**0.887**
	Hydroperiod	-0.399	-2.323	1.212	0.668
	Distance	-0.326	-1.538	1.380	0.736
Eurycea quadridigitata	**Canopy Cover**	**-0.496**	**-1.333**	**0.380**	**0.868**
	Hydroperiod	**-0.545**	**-1.674**	**0.430**	**0.848**
	Distance	**-0.857**	**-2.001**	**0.254**	**0.954**
Gastrophryne carolinensis	**Canopy Cover**	**-0.532**	**-1.782**	**0.713**	**0.805**
	Hydroperiod	-0.441	-1.614	0.739	0.778
	Distance	0.041	-0.875	0.936	0.533
Hyla avivoca	**Canopy Cover**	**-1.860**	**-5.459**	**1.276**	**0.894**
	Hydroperiod	-0.924	-3.844	1.773	0.752
	Distance	-0.562	-3.378	2.454	0.702
Hyla chrysoscelis	Canopy Cover	-0.093	-0.984	0.806	0.590
	Hydroperiod	**-0.775**	**-2.022**	**0.128**	**0.945**
	Distance	-0.273	-1.214	0.481	0.733
Hyla cinerea	Canopy Cover	0.126	-0.872	1.319	0.575
	Hydroperiod	-0.357	-1.417	0.604	0.776
	Distance	0.382	-0.457	1.642	0.764

Species	Species-specific parameter	Mean	95% CI		Bayesian p-values
Hyla femoralis	Canopy Cover	0.010	-1.008	1.381	0.541
	Hydroperiod	0.322	-0.738	1.694	0.687
	Distance	**0.519**	**-0.285**	**1.949**	**0.845**
Hyla gratiosa	Canopy Cover	-0.185	-1.047	0.619	0.677
	Hydroperiod	0.172	-0.666	1.141	0.635
	Distance	-0.242	-0.931	0.413	0.758
Hyla squirella	Canopy Cover	-0.313	-1.367	0.611	0.735
	Hydroperiod	0.129	-0.796	1.193	0.586
	Distance	0.141	-0.564	0.900	0.657
Notophthalmus perstriatus	**Canopy Cover**	**-1.168**	**-3.064**	**0.088**	**0.957**
	Hydroperiod	**-0.696**	**-2.325**	**0.482**	**0.851**
	Distance	-0.219	-1.264	0.564	0.673
Notophthalmus viridescens	**Canopy Cover**	**-0.705**	**-1.964**	**0.345**	**0.908**
	Hydroperiod	**-1.351**	**-3.394**	**-0.042**	**0.976**
	Distance	-0.418	-1.844	1.231	0.776
Pseudacris crucifer	**Canopy Cover**	**0.517**	**-0.566**	**1.717**	**0.826**
	Hydroperiod	0.413	-0.933	1.804	0.739
	Distance	-0.210	-1.368	0.998	0.657
Pseudacris feriarum	Canopy Cover	0.627	-1.411	3.032	0.764
	Hydroperiod	**-1.496**	**-5.490**	**0.664**	**0.900**
	Distance	0.007	-2.785	3.501	0.543
Pseudacris nigrita	Canopy Cover	0.304	-0.891	1.426	0.727
	Hydroperiod	**-1.017**	**-2.611**	**0.122**	**0.958**
	Distance	0.391	-0.674	2.239	0.713
Pseudacris ocularis	**Canopy Cover**	**0.968**	**-0.343**	**2.718**	**0.908**
	Hydroperiod	**-0.672**	**-2.594**	**0.937**	**0.812**
	Distance	**-1.038**	**-3.804**	**0.559**	**0.826**
Pseudacris ornata	Canopy Cover	0.241	-0.740	1.229	0.685
	Hydroperiod	**-0.533**	**-1.586**	**0.548**	**0.840**
	Distance	-0.261	-1.475	0.977	0.673
Pseudobranchus striatus	**Canopy Cover**	**-0.800**	**-2.947**	**0.786**	**0.840**
	Hydroperiod	**-0.815**	**-2.882**	**1.067**	**0.814**
	Distance	**-0.577**	**-2.139**	**0.863**	**0.838**
Rana capito	Canopy Cover	0.240	-0.906	1.441	0.655
	Hydroperiod	-0.260	-1.428	0.851	0.674
	Distance	0.019	-0.815	0.877	0.525

Species	Species-specific parameter	Mean	95% CI		Bayesian p-values
Rana catesbeiana	Canopy Cover	-0.163	-1.051	0.711	0.652
	Hydroperiod	-0.032	-0.862	0.785	0.535
	Distance	**-0.538**	**-1.487**	**0.331**	**0.892**
Rana clamitans	**Canopy Cover**	**0.346**	**-0.454**	**1.173**	**0.808**
	Hydroperiod	0.305	-0.534	1.115	0.765
	Distance	**-0.765**	**-2.215**	**0.500**	**0.872**
Rana grylio	**Canopy Cover**	**0.881**	**-0.296**	**2.206**	**0.920**
	Hydroperiod	-0.040	-1.139	0.960	0.517
	Distance	**-0.801**	**-3.061**	**0.817**	**0.819**
Rana sphenocephala	Canopy Cover	0.330	-0.622	1.404	0.732
	Hydroperiod	0.263	-0.630	1.228	0.716
	Distance	-0.171	-1.093	0.877	0.665
Scaphiopus holbrookii	**Canopy Cover**	**-0.753**	**-1.681**	**0.092**	**0.958**
	Hydroperiod	-0.233	-1.056	0.535	0.706
	Distance	**-0.604**	**-2.121**	**0.633**	**0.833**

Figures

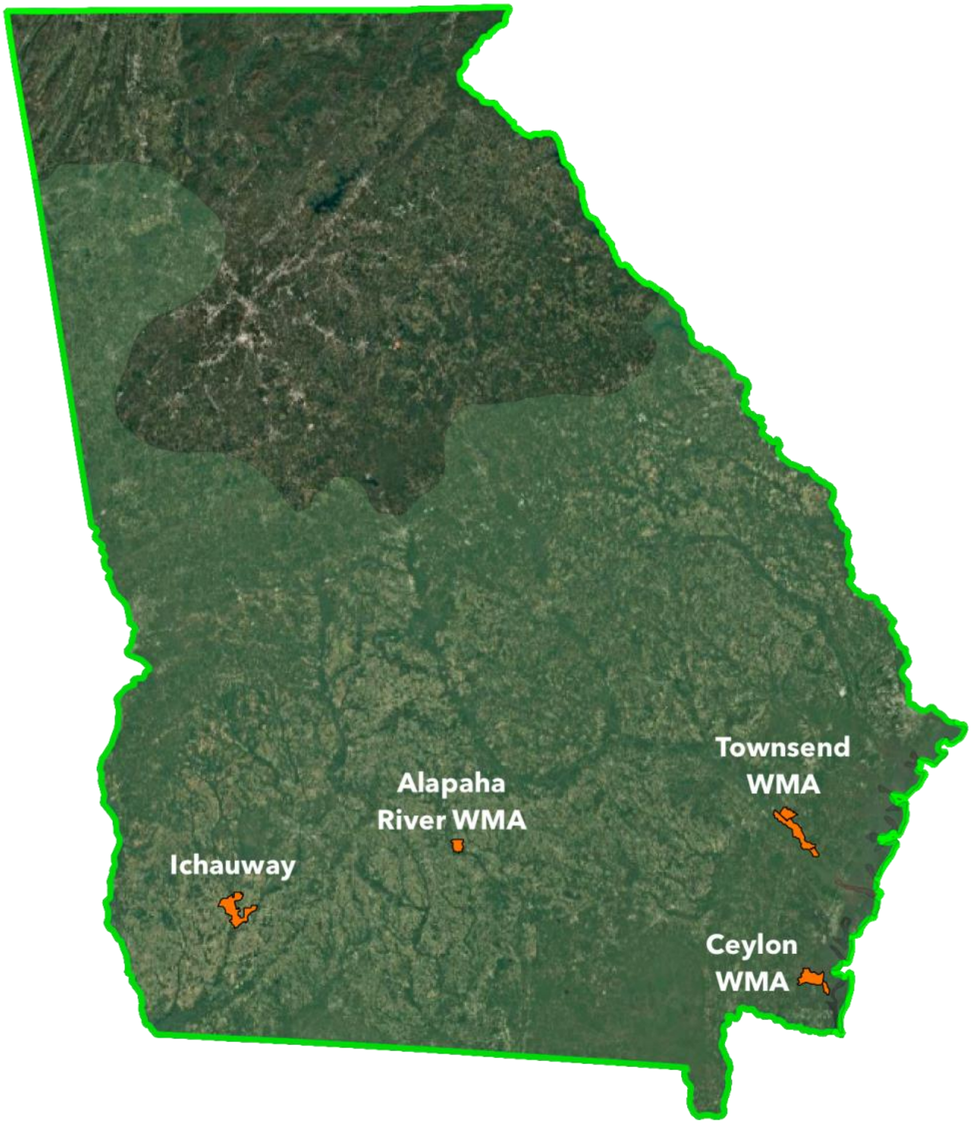

Figure 2.1. Map of Georgia, USA with the four focal study landscapes in orange. The Jones Center at Ichauway (Ichauway) located in Baker County, Georgia. Alapaha River Wildlife Management Area (WMA) located in Irwin County, Georgia. Ceylon WMA and Cabin Bluff located in Camden County, Georgia. Townsend WMA located in Long County and McIntosh County, Georgia. Light green shading represents the historic range of longleaf pine (Pinus palustris).

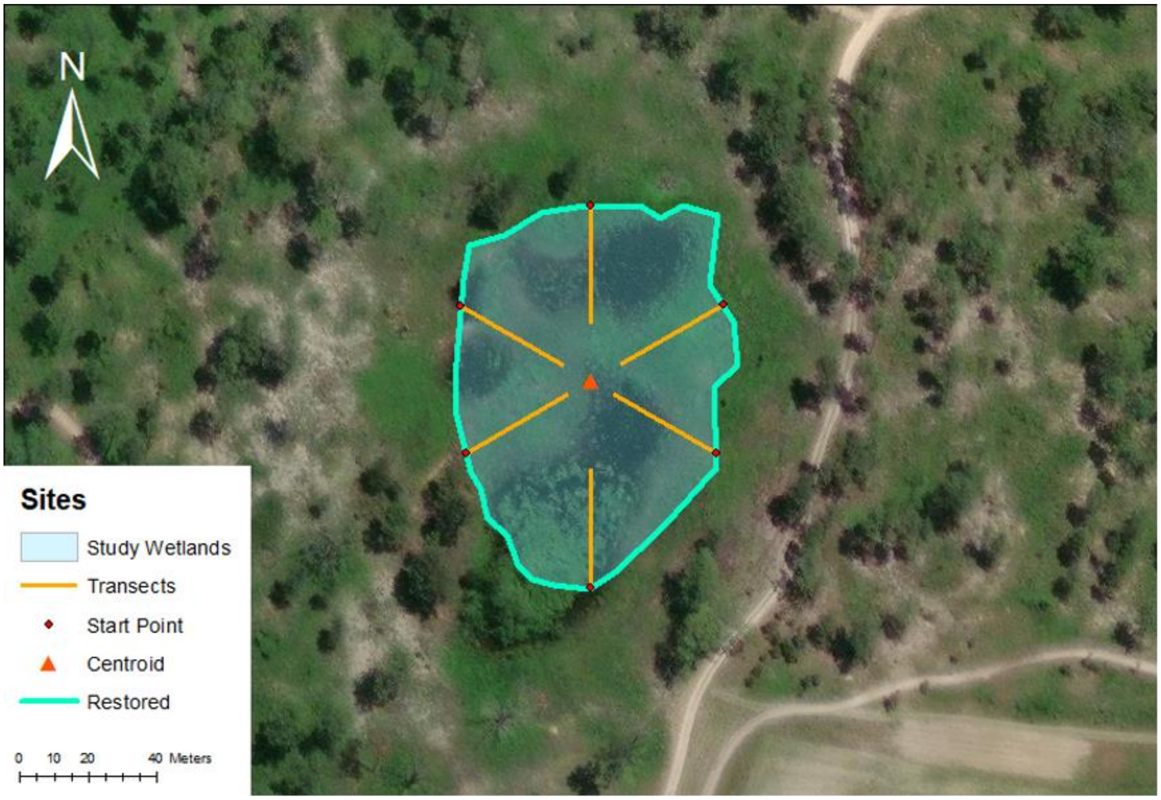

Figure 2.1. Map of a restored wetland on Ichauway and the transects sampled for vegetation surveys following Georgia Department of Natural Resources wetland restoration vegetation monitoring field protocol. Transects were arranged every 60 degrees and orientated towards the wetland centroid.

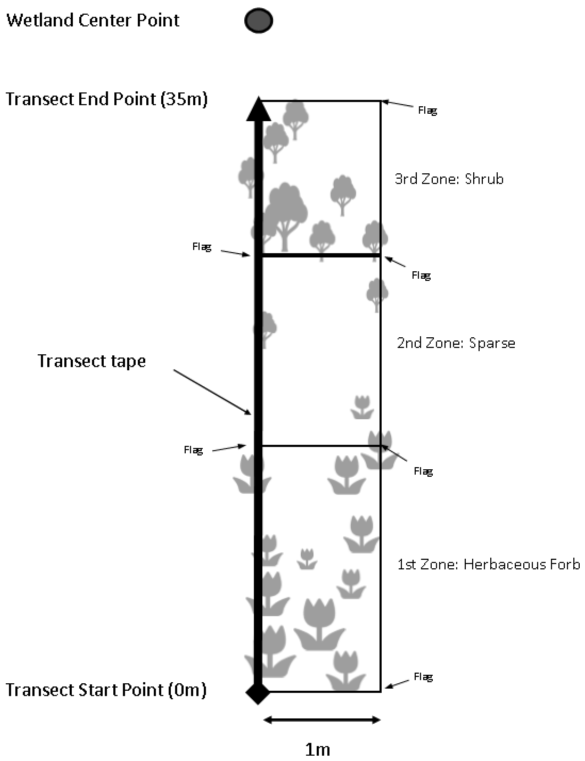

Figure 2.32. Overhead view of an example of a transect describing potential vegetative zones.

From Wetland Restoration Field Protocol, Source: Georgia Department of Natural Resources.

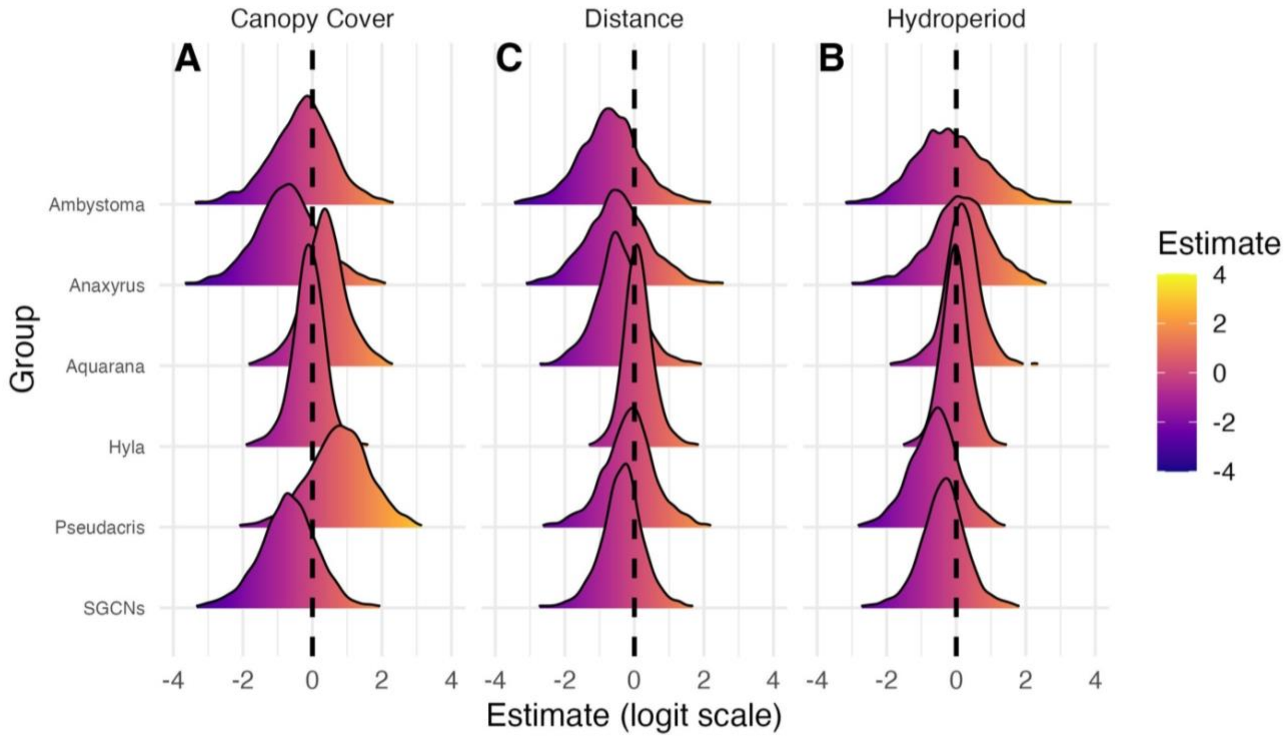

Figure 2.3. Posterior distribution of site covariates from an integrated Bayesian hierarchical on all occupancy covariates for amphibian group level responses in Georgia, USA. Estimates are on the logit scale.

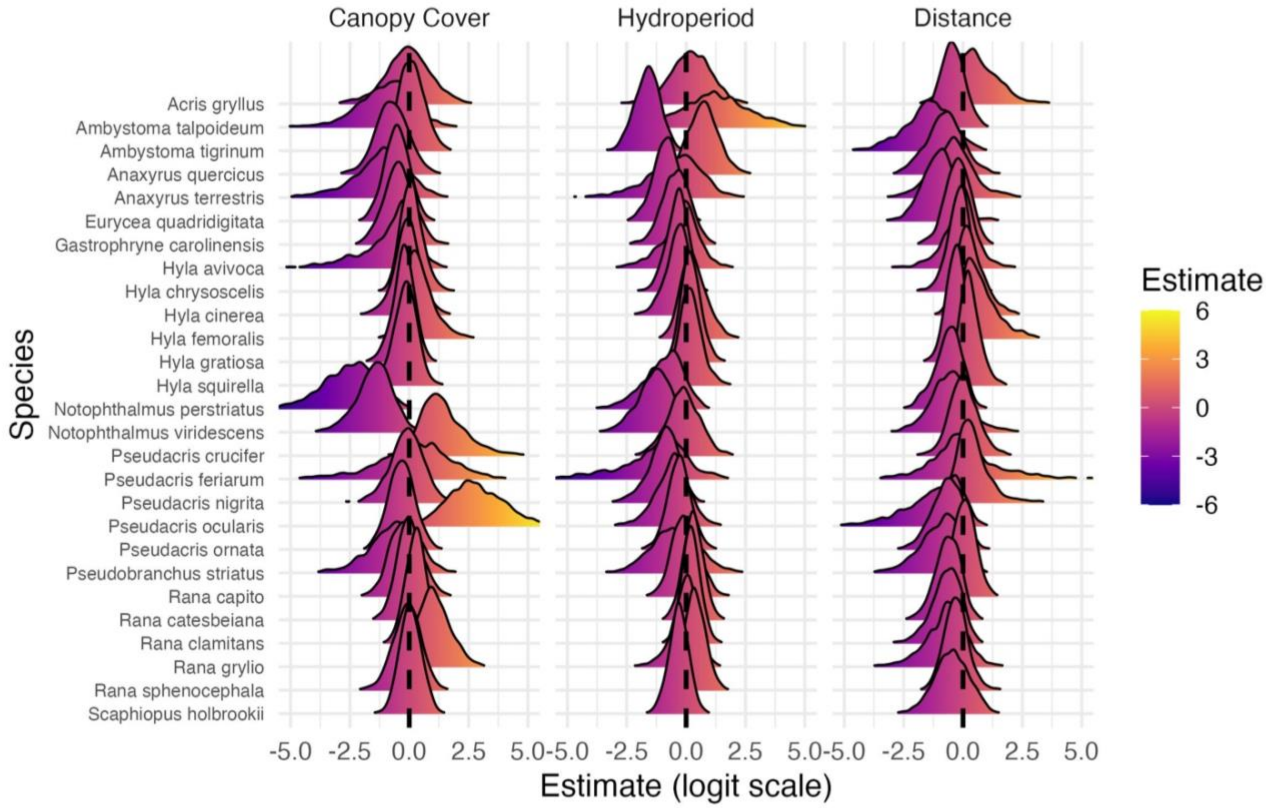

Figure 2.4. Posterior distribution of site covariates from an integrated Bayesian hierarchical community occupancy model (canopy cover, hydroperiod, and the number of nearby wetlands) on occupancy for amphibian species in Georgia, USA. Estimates are on the logit scale.

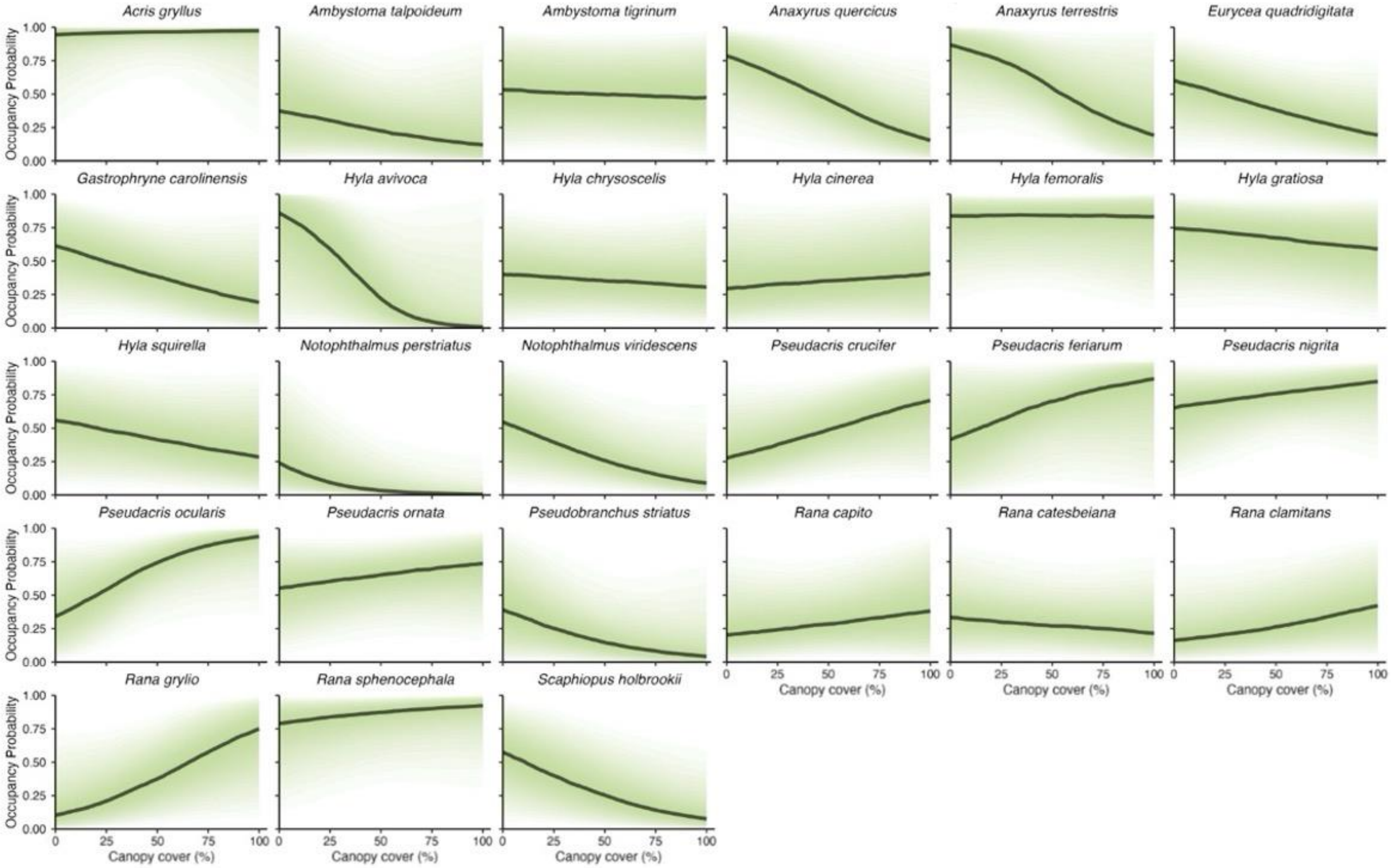

Figure 2.6. Mean species-specific estimates of occupancy probability for 15 amphibian species by canopy cover percent. Lines represent posterior means, and shaded ribbons show 95% (darkest) to 5% (lightest) credible intervals.

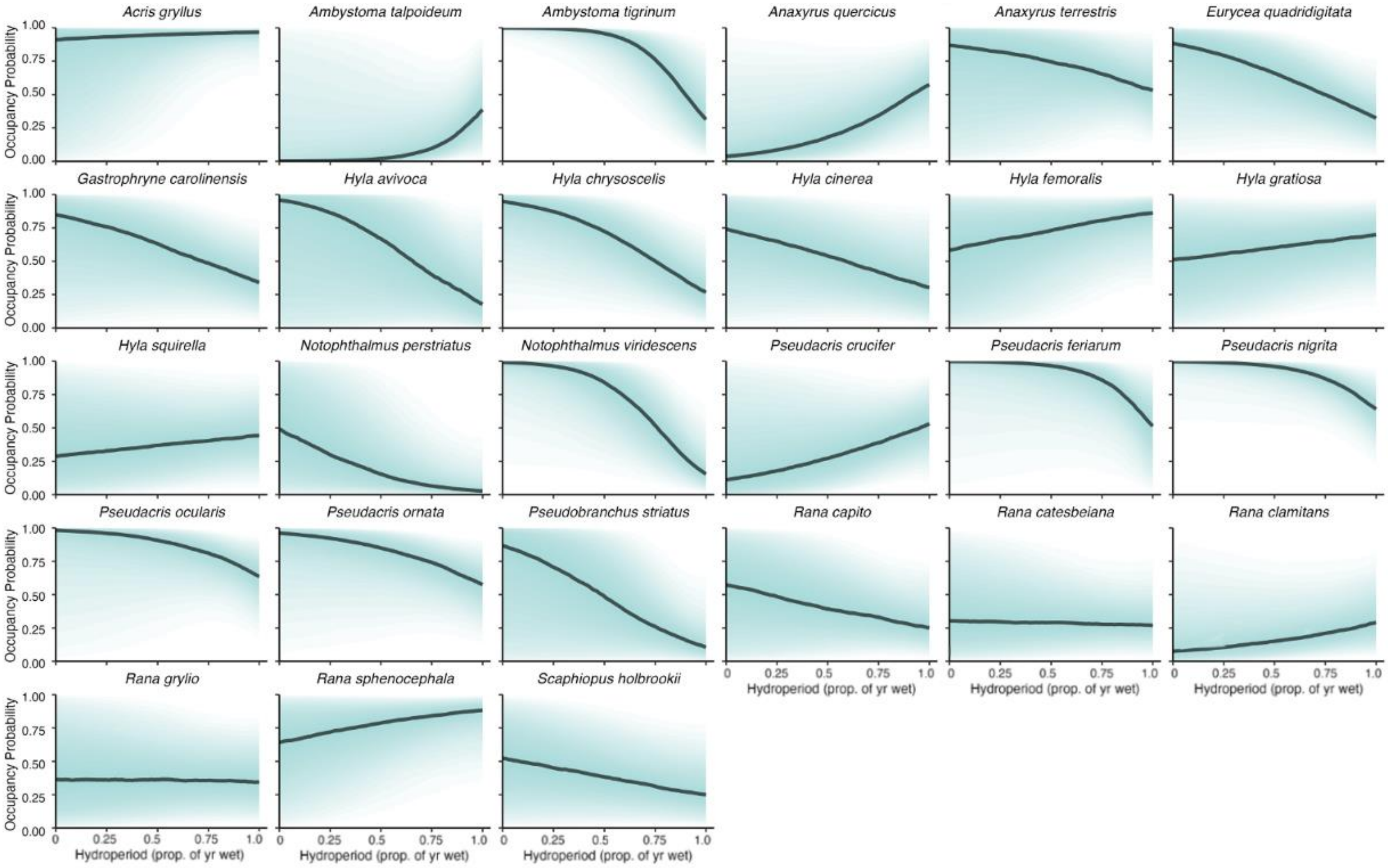

Figure 2.7. Mean species-specific estimates of occupancy probability for 27 amphibian species by hydroperiod. Lines represent posterior means, and shaded ribbons show 95% (darkest) to 5% (lightest) credible intervals.

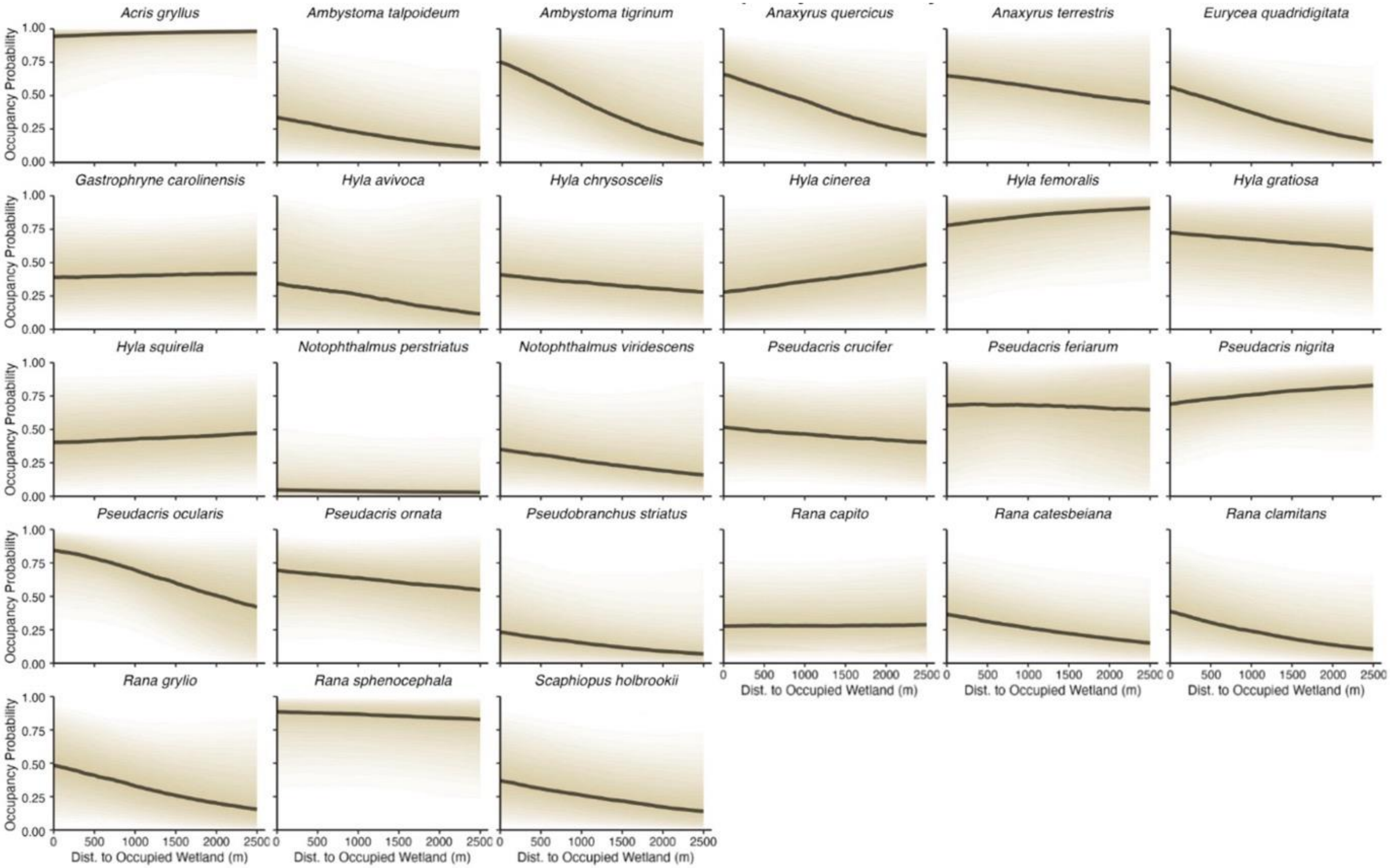

Figure 2.8. Mean species-specific estimates of occupancy probability for 27 amphibian species by distance to the nearest occupied wetland in meters. Lines represent posterior means, and shaded ribbons show 95% (darkest) to 5% (lightest) credible intervals.

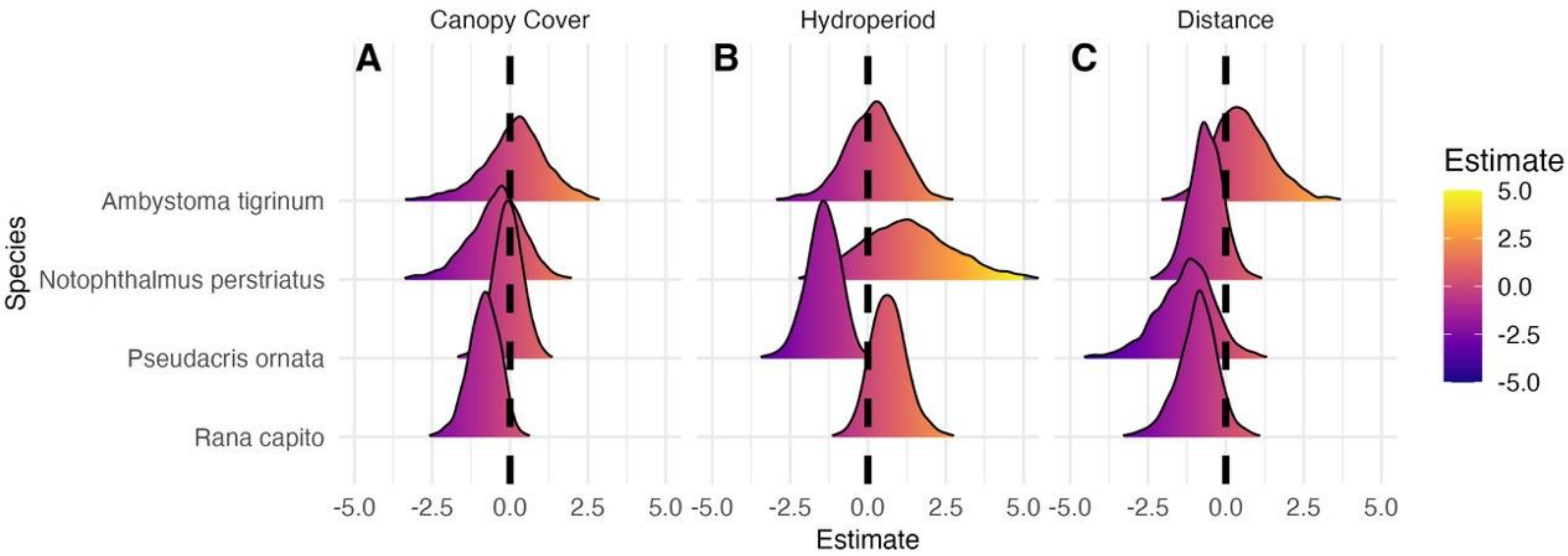

Figure 2.5. Posterior distribution of site covariates from an integrated Bayesian hierarchical on all occupancy covariates for amphibian species of conservation concern in Georgia, USA. Estimates are on the logit scale.

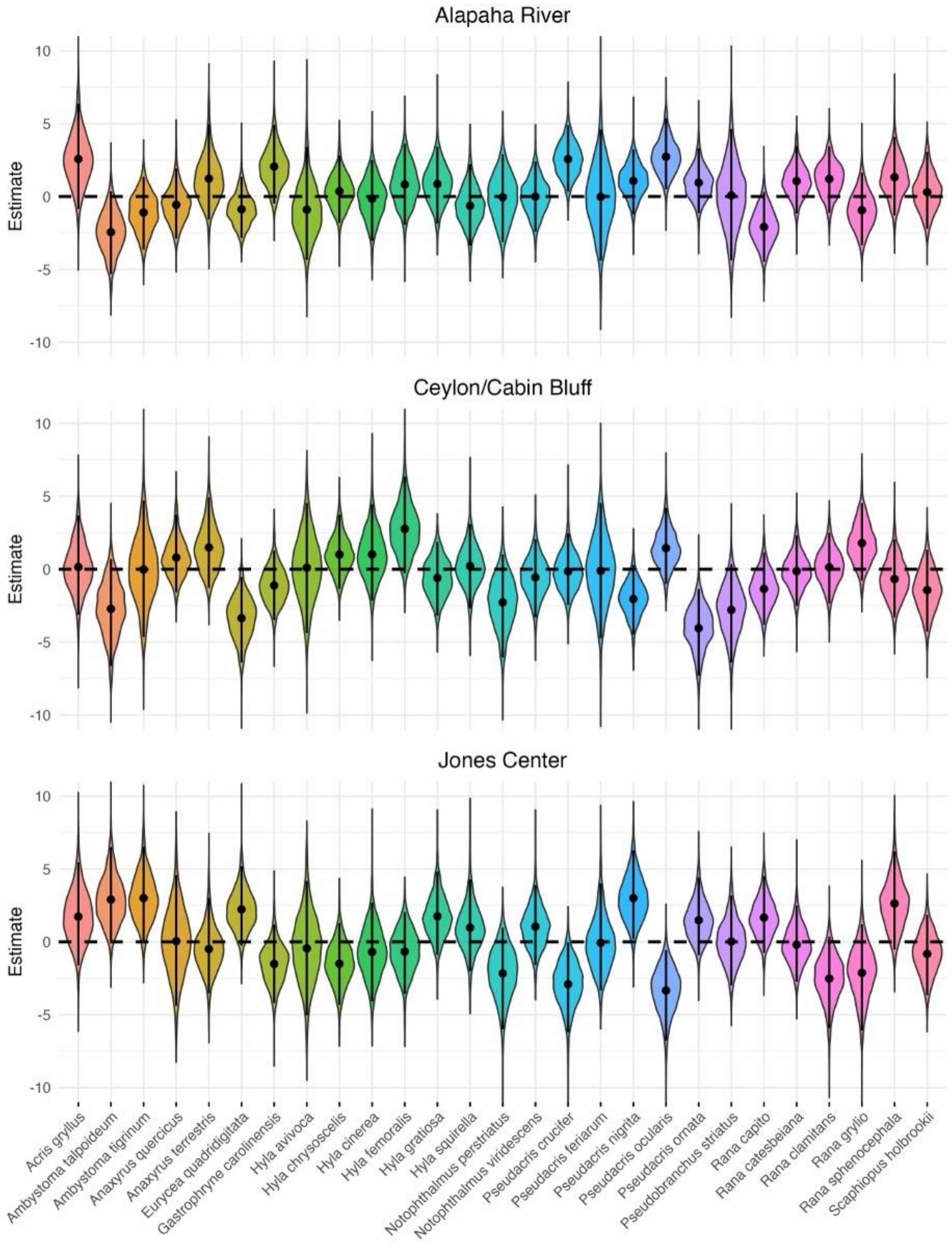

Figure 2.6. Posterior estimates of landscape as a random effect on all amphibian species across the four study landscapes. Estimates are on the logit scale.

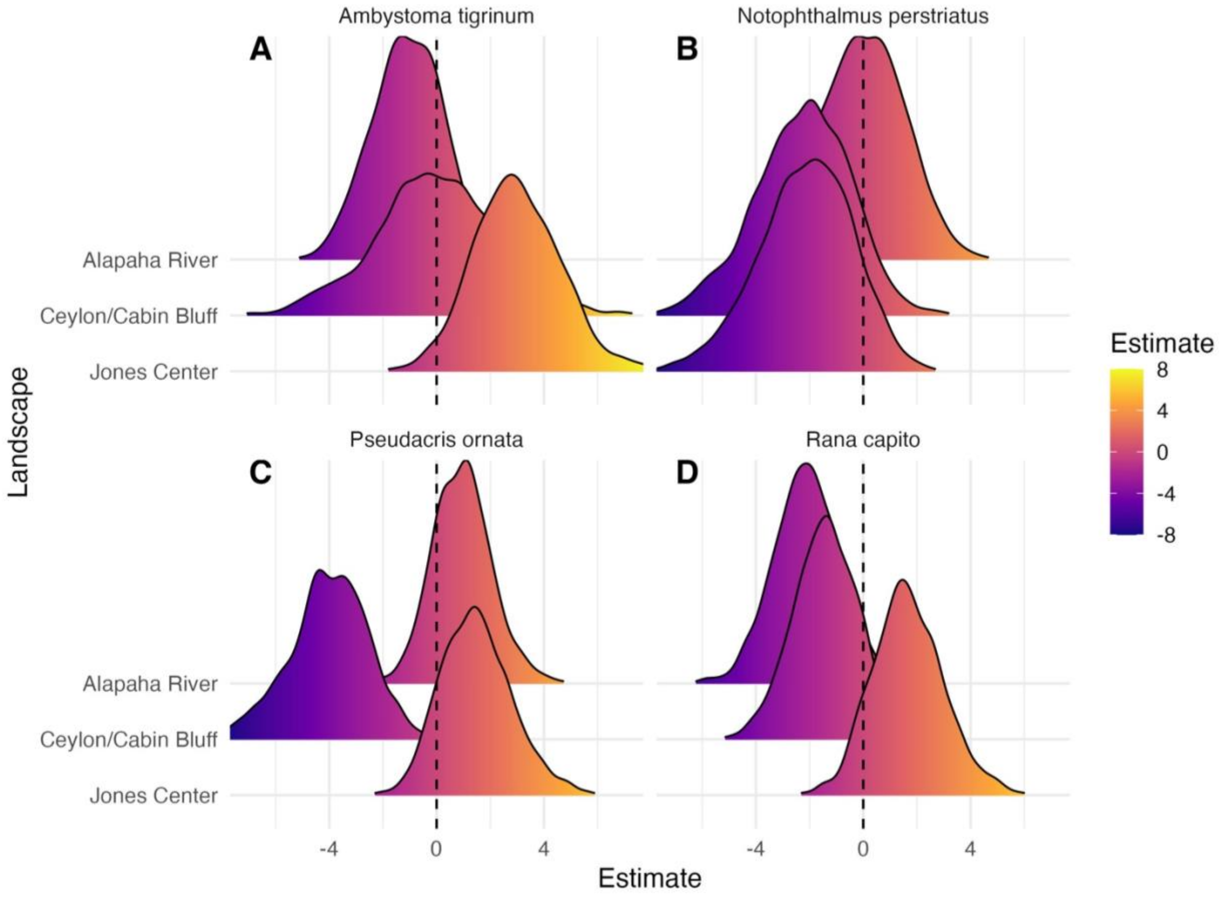

Figure 2.0.1. Posterior distribution of landscape as a random effect from an integrated Bayesian hierarchical on all occupancy covariates for amphibian species of conservation concern in Georgia, USA. Estimates are on the logit scale.

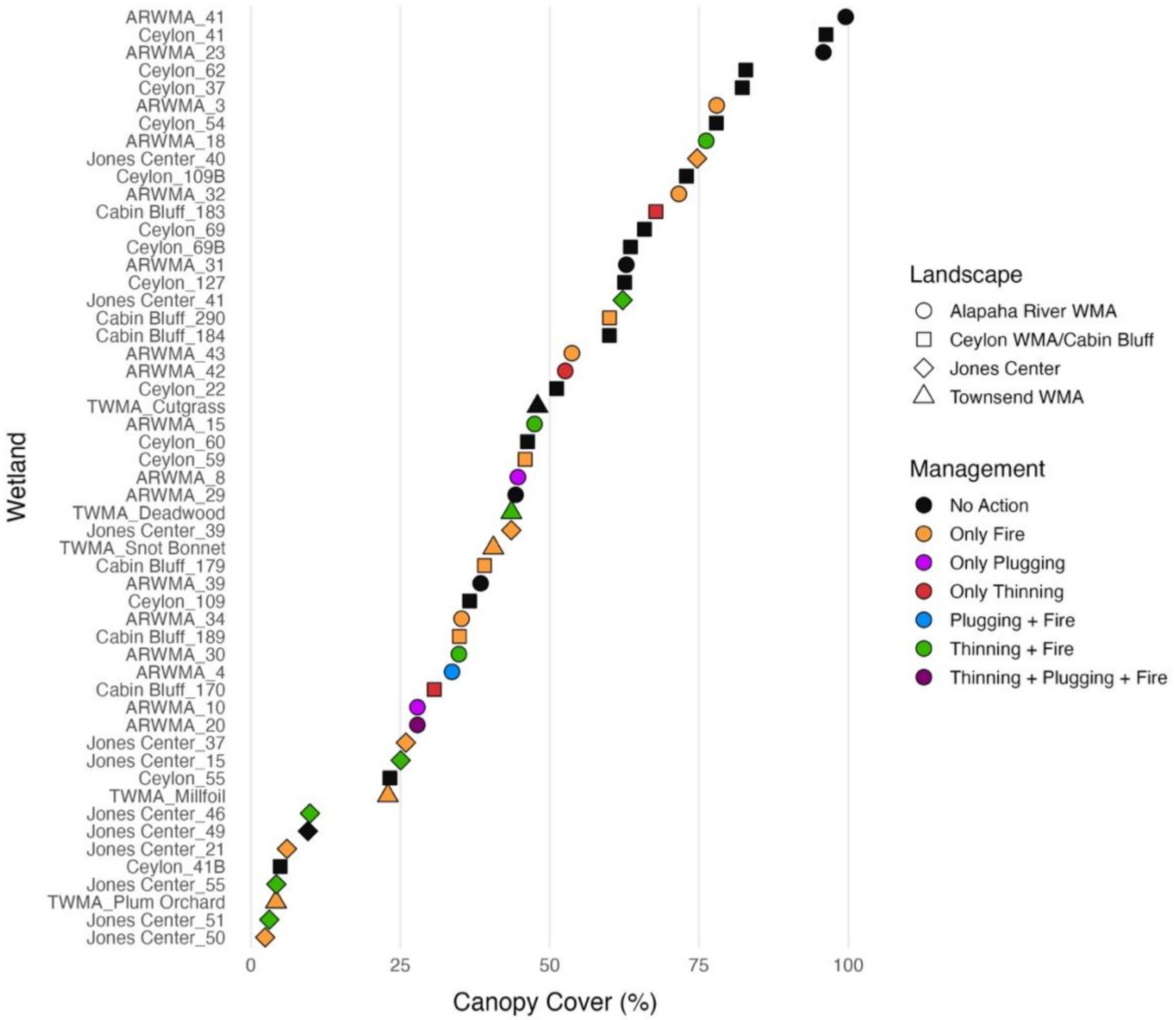

Figure 2.0.2. Canopy cover percentage of the study wetlands across the four focal landscapes. Symbol shape indicates the focal landscape and symbol colors indicate management actions taken within the wetland at some point since 2018.

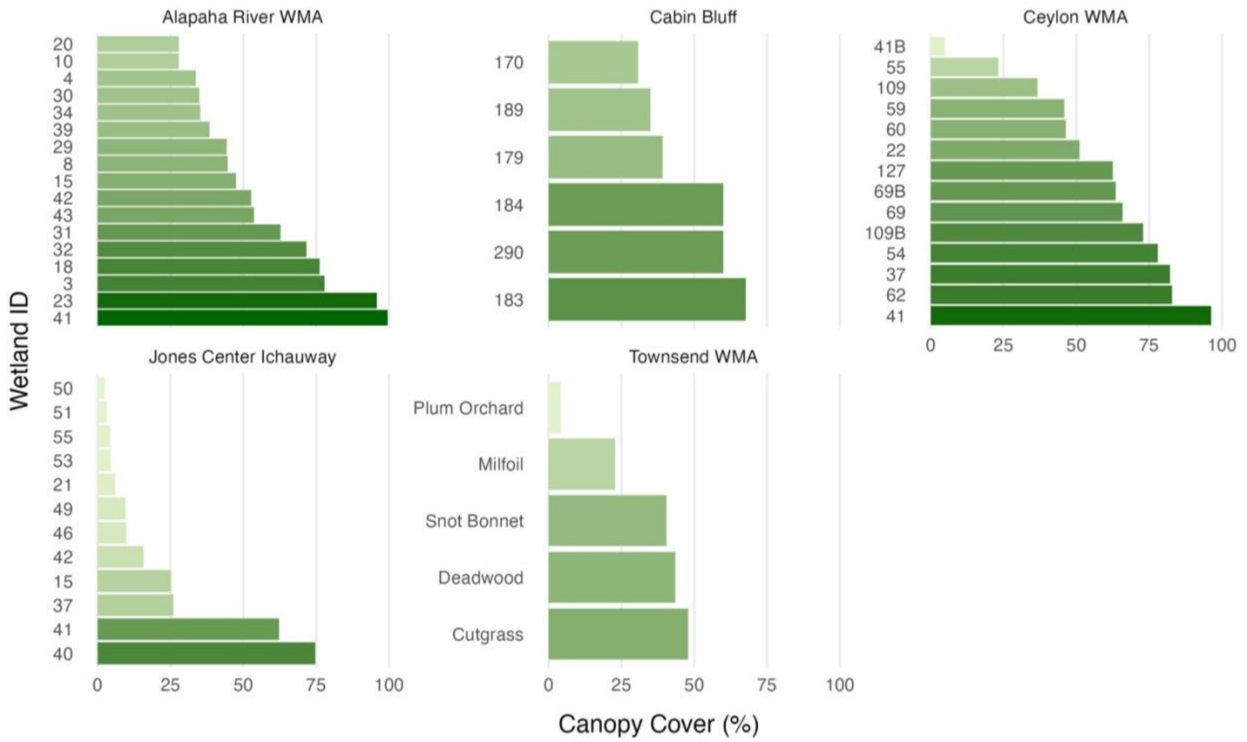

Figure 2.0.3. Variation in canopy cover percent among wetlands across study site. Bars represent individual wetlands, ordered by increasing canopy cover within each site. Shading intensity corresponds to canopy cover percent, with darker shades indicating higher canopy cover.

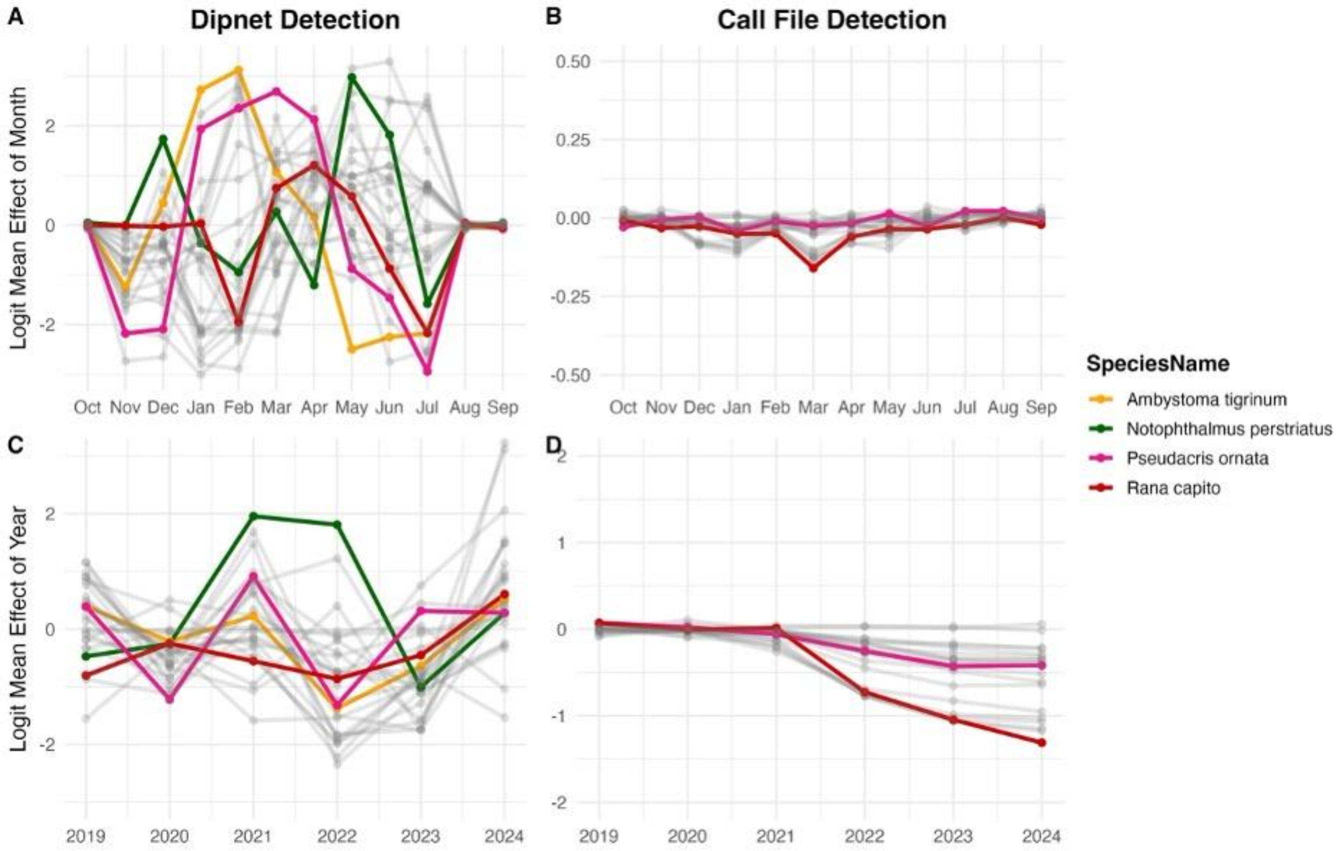

Figure 2.0.4. Mean estimated effect of month on species-specific amphibian detection dipnet surveys. B) Mean estimated effect of month on species-specific anuran detection for acoustic recording unit (ARU; call) surveys. C) Mean estimated effect of year on species-specific amphibian detection dipnet surveys. D) Mean estimated effect of year on species-specific anuran detection for acoustic recording unit ARU surveys. Focal species of conservation concern are depicted with yellow, green, pink, and red. All other species estimates are light gray.

CHAPTER 3

AN EXPERIMENTAL TEST OF SOFT RELEASE STOCKING DENSITY ON LARVAL SURVIVAL AND REPRODUCTIVE PATHWAY OF CAPTIVE-BRED STRIPED NEWTS[2]

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[2] Samples, J.A., J.C. Maerz, M. Cinello-Smith, E.O. Kerr, K. Hefferle, and L.L. Smith. To be submitted to a peer-reviewed journal.

Abstract

Habitat restoration alone is often insufficient for recovery of wildlife populations as restored sites are often geographically isolated from other populations. In these cases, translocations are necessary to supplement or re-establish populations; however, many translocation projects lack rigorous experimental design, standardized monitoring, or defined objectives, resulting in outcomes that are difficult to assess. Ideally, the success of translocations is evaluated in stages: (1) survival of the release generation; (2) reproduction by the release generation and their offspring; and (3) persistence of the resulting population through time. The use of soft-release strategies can improve translocation success and post-release monitoring. In 2024, we used an experimental framework with soft-release enclosures to evaluate stocking density effects on translocation outcomes for 116 captive-reared, 1-12 month old larval Striped Newts (*Notophthalmus perstriatus*) translocated into a 0.89 ha seasonally inundated wetland. Newts were individually marked, measured, and randomly assigned to enclosures at low (9), medium (17), and high densities (32) based on life stage, size, and sex. Newts were released in February and monitored monthly through September 2024 using dipnet depletion surveys in enclosures to estimate individual survival of newts, first generation reproduction, and second-generation recruitment and reproduction. Even within soft-release enclosures, detection probability of newts was low and negatively correlated with water depth, highlighting the general difficulty of detecting this species. Survival probability of the translocated newts was generally high, with evidence of a positive effect of larval body size at release on survival. There was moderate evidence of a negative effect of high stocking density on survival. Most larvae developed into paedotypic adults within two months of release, and we detected viable eggs and larvae. Once we detected first generation eggs and larvae in exclosures, we removed the adults from half the enclosures and left adults in the other half to determine whether cannibalism might affect larval recruitment. We only detected larval recruitment in the medium stocking density enclosure where we had removed the older conspecifics. Second generation larvae grew and matured into paedotypic adults in under one year. Our results indicate that soft-release methods and release of larger, late-stage larvae can enhance post-release survival, promote paedotypy, and facilitate early reproduction and rapid recruitment of Striped Newts.

Introduction

Habitat restoration is a foundational management action to stabilize, recover, and increase rare wildlife populations (Morrison & Mathewson, 2015). Yet, natural ecosystems are complex, and many factors can constrain the success of restoration efforts. Biotic responses often lag behind management actions (Cosentino et al., 2024; Bond and Lake, 2003;Brown, 2023; Vesk et al. 2008), and latent constraints like extinction debt, genetic bottlenecks, inbreeding depression, and inverse density dependence (Allee effects) may drive continued declines despite improved habitat quality (Dennis, 1989; Hylander & Ehrlén, 2013; Nieminen et al., 2001). These processes are particularly concerning for rare species that persist in a small number of remnant habitat patches and metapopulations. Persistence within these patches is dependent on patch quality and area, interpatch distance, landscape permeability, and species dispersal capacity (Brooks et al., 2002; Fahrig, 2013; Hanski & Ovaskainen, 2000; Tilman et al., 1994). For dispersal-limited species, recolonization of isolated, restored patches may be unlikely without intervention (Lehtinen & Galatowitsch, 2001). Thus, the intentional movement of wild or captive-bred individuals (“translocations”) (IUCN, 1987) is frequently paired with habitat restoration to recover and sustain wildlife populations (Seddon et al., 2007).

In practice, translocation programs have yielded mixed results, and many sources of uncertainty make evaluations of success difficult (Gould et al., 2023; Miller et al., 2014). It seems intuitive that the ultimate goal of translocations, the release of individuals into an area where they formerly or currently occupy (Dodd & Seigel, 1992), is to establish self-sustaining populations. However, members of the 7th World Conference on Breeding Endangered Species (Seddon, 1999) cautioned that this definition of success is problematic. They proposed that the success of translocations be evaluated in both short to longer term milestones such as: (1) survival of the release generation; (2) breeding by the release generation and their offspring; and (3) persistence of the re-established populations, perhaps assessed through population viability analysis. Species-specific biological constraints such as density dependent processes and dispersal limitations can influence the near-term performance of translocated individuals and the longer-term persistence of translocated populations (Converse et al., 2013; Dodd & Seigel, 1992; Folt et al., 2019; Gould et al., 2023). Because the focal species for translocation projects are typically threatened or endangered, there are often uncertainties regarding the presence of limiting life history traits and low detection probabilities following release (Folt et al., 2019; Wendt et al., 2021). Therefore, more work is needed to understand the biological constraints for translocated organisms through controlled experiments as well as targeted monitoring of release strategies.

Adaptive Management: Pushing the Boundaries of 'Best Practice'

The outcomes of translocations are strongly influenced by the selection and design of appropriate release methods (Batson et al., 2015; Resende et al., 2021). Because translocations are inherently complex (Armstrong & Seddon, 2008; Ewen & Armstrong, 2007), effective strategies must be tailored to specific species, sites, and conservation objectives. Yet, many translocation projects lack defined objectives, rigorous experimental design, or standardized monitoring, resulting in outcomes that are often anecdotal and difficult to compare (Armstrong & Seddon, 2008; Berger-Tal et al., 2020; Seddon et al., 2007). As a result, there is little opportunity to accumulate evidence on drivers of success or failure (Lloyd et al., 2019; Romesburg, 1981). Adaptive management addresses these limitations by embedding monitoring and learning into the decision-making process to facilitate continual refinement (Canessa et al., 2019; Lyons et al., 2008; Williams & Brown, 2018). For translocations, this requires linking management actions to measurable objectives (target occupancy, population sizes, or measures of recruitment over defined spatial and temporal scales) and deliberately varying methodologies to test hypotheses and reduce uncertainty (Cowen, Richards, et al., 2025; Ewen & Armstrong, 2007). Statistical and predictive models then can be used to estimate the consequences of alternative strategies and to investigate the effectiveness of current practices (McCarthy et al., 2012). An experimental framework for translocations is essential to building an evidence base for refining strategies over time (Cowen, Buckley, et al., 2025).

An Experimental Approach to Release Strategy: The Striped Newt

The Striped Newt (*Notophthalmus perstriatus*) is a state-threatened species in Georgia and Florida that exemplifies both the challenges and opportunities of applying adaptive management to wildlife translocations. Only four or fewer extant populations remain in Georgia (Georgia SWAP, 2025; Farmer et al., 2017), with only one robust population currently known and restricted to a single wetland on a state-owned Wildlife Management Area (Navis, 2025). Most other known populations on public or privately managed conservation lands are either likely extirpated or exist at very low abundance, such that they are highly vulnerable to stochastic extinction. The main driver of Striped Newt declines is presumed to be habitat loss, particularly the conversion and use of terrestrial habitats around wetlands for intensive forestry or agriculture and the draining or degradation of GIWs. However, Striped Newt populations continue to decline and go extinct on large, managed landscapes. The causes of these Striped Newt population declines remain unclear but may be connected to disruption of metapopulation dynamics, habitat degradation, and climate change. Striped Newts population dynamics appear particularly sensitive to wetland hydroperiod and canopy closure, thus it is presumed that continued declines on managed landscapes have been driven by remnant wetland habitat degradation and increasing drought frequency.

In response to the precarious status of Striped Newts, state agencies and numerous conservation organizations have developed captive-breeding programs using wild-caught founders, with the goal of releasing captive-produced Striped Newts into restored wetlands within their historic range (Georgia SWAP, 2025). The long-term success of these initiatives will depend on addressing ecological uncertainties and refining release strategies through targeted monitoring and research. Success of previous Striped Newt translocations in Florida has been difficult to assess because newts were released directly into wetlands (hard releases). These releases have yielded very few detections of newts, and it cannot be determined whether this reflects mortality, emigration, or low detection (R. Means, personal communication, 2024).

Recent work by Navis and Maerz (2025) has shown that in isolated wetlands with long hydroperiods in Georgia, Striped Newt larvae tend to develop into paedotypic adults within their first year, driving rapid recruitment and population growth following pond drying event. This process is likely critical to sustaining robust newt populations and suggests that the release of intermediate to late-stage larvae may be most effective for establishing populations (Johnson 2002). Collaborators at the Atlanta Botanical Garden have improved the husbandry of captive-reared newts such that they can produce later stage larvae that retain their gills (Thomas et al., in press). However, it is unknown whether these larvae will remain paedotypic post-release and whether survival and life history pathways are density-dependent. Amphibians with complex life cycles often exhibit strong density-dependence, particularly within aquatic larval or adult life stages, and translocation outcomes may vary across stocking densities. Low densities may lead to negative effects on recruitment or increased stochastic failure (Allee effects). High densities may increase competition among larvae, reducing their fitness or shifting them into developmental pathways other than paedotypy, which do not yield rapid population growth. In Broken-Striped Newts (*Notophthalmus viridescens doralis*), larval density strongly influences growth, sexual maturity, and life-history trajectories (Harris, 1987), but no such *in situ* data exists for Striped Newts. The evaluation of soft release strategies and stocking densities on the development and reproduction of captive-bred Striped Newts could substantially improve translocation success.

The main objectives of this study were to 1) use soft-release of captive-born larval newts to estimate the effect of stocking density and body size at release on survival (Seddon 2010, criteria 1) and probability of remaining in a paedotypic form, and 2) describe the apparent effects of stocking density on reproduction during the first breeding season after release, and potentially on the recruitment, survival, and breeding probability of second-generation individuals (Seddon 2010, criteria 2). We used soft-release enclosures to increase detection during post-release monitoring and to control stocking density. We hypothesized that survival and reproduction would differ among stocking densities, with highest success at moderate densities due to competition effects at high densities and inverse density dependence at low densities. We also expected, based on Navis' (2025) findings, that larger, late-stage larvae were more likely to remain paedotypic after translocation than smaller larvae. Since captive husbandry practices typically involve removing Striped Newt adults after reproduction as a precaution against cannibalism (Thomas C., personal communication), we also examined the potential for the presence of larger related and non-related conspecifics to cannibalize and therefore negatively affect larval survival under more natural conditions.

Methods

Study Site

The Jones Center at Ichauway (hereafter Ichauway) is an 11,700-ha private research facility in Baker County, Georgia, USA. The property has been managed for Northern Bobwhite hunting since the 1920s, and has second-generation longleaf pine stands with both native and old field ground cover. Ichauway is in the Dougherty Plain, a subregion of the Coastal Plain characterized by karst topography and limestone sinks, responsible for the more than 100 depressional, seasonal geographically isolated wetlands (GIWs) on the property. Historically, longleaf pine uplands and GIWs across the Southeastern U.S. was among the most species-rich habitats in North America (; Snodgrass et al., 2000). Longleaf pine forests and the embedded GIWs at Ichauway continue to support high plant and animal diversity despite recent (1980s) large-scale agricultural development of surrounding lands (Smith et al., 2006). However, several species including Striped Newts, which were historically recorded from four wetlands at Ichauway were last detected in 2006 and are believed to be extirpated following a series of prolonged droughts in which Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) also disappeared from the property (Farmer et al., 2017). All terrestrial habitats at Ichauway are managed with prescribed fire on a 1-2 year return interval. Wetlands burn periodically when adjacent uplands are burned when the wetlands are dry. However, mechanical and chemical reduction of woody encroachment within and around wetlands has been increasingly used to restore vegetation structure. In 2023, Ichauway partnered with the Atlanta Botanical Garden to start Striped Newts repatriation effort in some of the historic and recently restored wetlands.

For this study, the release wetland was a 0.89 ha seasonally inundated depressional marsh wetland (Golladay et al., 2021; Kirkman et al., 2000) with an open canopy, grass-sedge dominance, and patches of Buttonbush (*Cephalanthus occidentalis*). The release wetland, though not a known historic Striped Newt wetland, has undergone extensive restoration in the basin as well as thinning in the uplands since 2009 (Golladay et al., 2021). We chose the release wetland based on the consistent hydroperiod and successful recruitment of other amphibian species associated with Striped Newt breeding sites or with comparable habitat requirements (e.g., Eastern Tiger Salamander (*Ambystoma tigrinum*), Eastern Newt (*Notophthalmus viridescens*), and Gopher Frog (*Rana capito*) (Atkinson et al. 2021).

Data Collection

On October 5, 2024, we released 116 captive-born, Striped Newts of varying sizes and sexes into six 1.5 x 1.5m soft-release enclosures. All Striped newts were produced and reared until release at the Atlanta Botanical Garden. We constructed the enclosures with frames made with 5 cm diameter Polyvinyl chloride (PVC) pipes lined with nylon window screen mesh (18 x 16 threads per inch) that was hand sewn to enclose the bottom and sides of the enclosure (Figure 3.1). The screen mesh and open tops of the enclosures permitted natural colonization by prey, predators, and wetland vegetation. We supplemented each enclosure with additional native wetland vegetation, including Lesser creeping rush (*Juncus repens*) and Watershield (*Brasenia schreberi*) to promote the growth of natural refugia, shade, and oviposition sites for newts. We installed the enclosures at similar depths (~40 cm) in the deepest part of the wetland to reduce the risk of early drying and to provide broader thermal gradients for newts to thermoregulate (Figure 3.1).

We randomly assigned each enclosure one of three stocking densities levels (low, medium, high). There were two replicates at each density for a total of six enclosures. We stratified newts based on size and – for those individuals beginning to show secondary sexual characters – sex (Table 3.1). We uniquely marked the newts with Visual Implant Elastomer (VIE; Northwest Marine Technology Inc., Anacortes, WA, USA) tags (Grant, 2008), measured, and assigned individuals to enclosures at one of three densities using a stratified random assignment based on life stage, size, and sex (Table 3.1). There was some variation in newt developmental stages; however, 93.9% were gilled larvae or premature adults that had undergone incomplete metamorphosis (paedotypes). Low density enclosures had 9 newts (4 newts/m2), medium had 17 (7.6 newts/m2), and high density enclosures were assigned 32 newts (14.2 newts/m2). We were limited in the possible combinations of sex and age classes based on availability. We applied consistent rules to ensure comparable demographic structure across enclosures. Each enclosure was stocked with at least two adult females and two adult males. Across density levels, we approximately doubled the number of females at each step (low: 2; medium: 5; high: 10). Adult males were allocated at roughly half the number of females within each density level, except for the low-density enclosures, which contained two males. All remaining individuals within each enclosure were juveniles.

We monitored the newts within the soft-release enclosures monthly via depletion sampling (Petranka & Murray, 2001) using a 3.2 mm mesh dipnet to estimate survival, growth, and reproduction. Observers completed four full passes where each pass included dipnetting the entirety of the enclosure. We recorded the individual ID, life stage (larval, eft, or reproductive adult) based on the presence of secondary sexual characters, sex, categorical gill length (0-3), snout-to-vent length (SVL), and total length of each newt recaptured during at each sampling occasion. We also recorded the maximum water depth in the enclosures during each sampling occasion. During monthly monitoring of enclosures, we also examined vegetation for newt eggs and removed and released Striped Newts that had absorbed their gills and transformed into a juvenile eft or terrestrial adult life stage to prevent drowning.

The presence of eggs or unmarked larvae (F1s) was used to confirm reproduction by stocked newts. We did not mark the F1 larvae due to their small body size, but we returned them to enclosures for future monitoring of F1 growth, development, and recruitment as adults. One month after the first detection of reproduction, we removed all marked newts from one replicate enclosure of each stocking density. We relocated those older individuals to new enclosures (Figure 3). Because newts are known to cannibalize larvae, our goal was to investigate whether the presence of larger conspecifics in soft-release enclosures would reduce larval recruitment. After seven sampling events between February and October 2024, rapid drying of the wetland prompted the release of the newts from the enclosures into the wetland. We conducted a final dipnet depletion survey and released all remaining individuals. We considered any newts that were not recovered and removed from enclosures as having died in the enclosures during the study period.

Data Analysis

We used a modified Cormack Jolly Seber (CJS) open-population model implemented in a Bayesian framework to estimate apparent survival (ϕ) and recapture probability (p) of the soft-released Striped Newts. The open-population CJS model accounts for imperfect detection while allowing survival probability to vary among individuals. We formatted the capture histories to include replicate dipnet "passes" to improve detection estimates such that if individual i, was detected at sampling event t, on pass d, $y_{i,t,d}$ equaled one; other $y_{i,t,d}$ equaled zero. We parameterized the model in discrete-time intervals that corresponded to each sampling occasion. Since the enclosures were closed systems for Striped Newts, we assumed that site fidelity within enclosure was to equal one and did not include permanent emigration or a spatial component in the model. However, undetected escape events could not be distinguished from mortalities in the model and therefore both were modeled as apparent survival failures (Schaub & Royle, 2013).

We modeled the latent state $z_{i,t}$ such that if individual i was alive and recaptured on sampling occasion t, $z_{i,t}$ equaled one; otherwise $z_{i,t}$ equaled zero. We considered the latent state $z_{i,t}$ to be a Bernoulli random variable:

$$z_{i,t} \sim Bernoulli\ (z_{i,t-1} * \phi_i * Available_{i,t} + \left(1 - Available_{i,t}\right)) \ ,$$

We modeled ϕ_i is the apparent survival probability for individual i. We included an availability mask to ensure survival and detection were estimated only when individuals were present in the enclosure. The availability mask prevented the model from interpreting the released efts as apparent mortalities.

We modeled individual apparent survival probability (ϕ_i) as a linear logit function of the covariates:

$$logit(\phi_i) = \alpha_0 + \alpha_1 * ReleaseSVL_i + \alpha_2 * StockingDensity_i + u_{enclosure[i]}$$

The covariate release SVL was the individual's body size measured as snout-to-vent length in millimeters at the time of the release. We defined stocking density as the initial number of newts in the individual's enclosure. We included enclosure as a random effect to account for variation among enclosures.

We modeled capture probabilities as a logit linear function of the model covariate depth:

$$logit(p_{i,t}) = \beta 0 + \beta 1 * depth_{i,t}$$

The covariate depth was the maximum water depth in centimeters in the enclosure during the sampling occasion. We centered and scaled all covariates. We implemented the model in JAGS using the package "rjags" (R Core Team 2014). We ran three MCMC chains for 20,000 iterations, discarded the first 10,000 as burn in, and thinned the chains by a factor of 10. We assessed convergence using Gelman-Rubin test (R <1.1) and visual inspection of the trace plots.

We also used a Bayesian generalized linear model to estimate effects of body size at release and stocking density on probability of paedotypy (the probability of transforming into, or retaining, larval traits into sexual maturity) among survivors. Based on our sample size, we chose a Bayesian approach because it allowed us to quantify uncertainty with posterior distributions and generate credible intervals for effect sizes. We parameterized the model as Bernoulli distributed outcome with a logit-link function of the covariates. For survival, we defined a binary indicator for each individual i, where $Survived_i$ equaled one if the individual was alive at the last sampling occasion or released; otherwise $Survived_i$ equaled zero.

$$Paedotypy_j \sim Bernoulli(p_{paedotypy,j})$$

$$logit(p_{paedotypy,j}) = \beta_0 + \beta_1 * ReleaseSVL_j + \beta_2 * StockingDensity_j + u.tank_{tank[i]}$$

Where we defined release SVL as the individual's body size measured as snout-to-vent length in millimeters at release and stocking density as the number of newts released into the individual's enclosure. We also added a random effect of tank for each individual's enclosure to account for enclosure-level variation. We centered and scaled covariates prior to analysis. We implemented the model in JAGS via the package rjags (R Core Team 2014). We ran three Markov chain Monte Carlo (MCMC) chains for 15,000 iterations, discarding the first 2,500 as burn-in and thinned the remainder by a factor of 2. We assessed convergence using Gelman–Rubin statistics (R-hat<1.1) and by visual inspection of the trace plots.

Results

The length of the sampling period (February-October) was eight months with seven sampling occasions. In February, the maximum water depth in the study wetland was 48cm. Water depth increased over time and reached a maximum depth of 95 cm in May after a large rain event, then receded quickly in September down to 26 cm as the wetland dried. We estimated that 75.4% of the released newts survived to the final sampling occasion (Table 3.2). Among survivors, 76.7% were paedotyic adults that retained larval traits including the presence of external gills (Table 3.3). At the final sampling occasion, we observed some newts exhibiting morphological indicators of metamorphosis, including partial external gill and tail fin reabsorption and the development of granular skin, consistent with transition to a terrestrial life stage (Walters & Greenwald, 1977). The number of individuals that metamorphosed into either efts or terrestrial adults varied by enclosure and stocking density. All enclosures had two individuals metamorphose, except for the high density treatments, where one enclosure produced a single metamorphosed individual and the other produced seven.

We observed our first evidence of reproduction in April during the second dipnet survey, when we detected recently deposited eggs attached to Lesser Creeping Rush in three soft release enclosures. We transported the eggs, still attached to the vegetation, back to the lab for observation. Once confirmed to be Striped Newts following hatching, we returned the larvae

(F1s) to their original enclosures. Reproduction was further confirmed in June during the fourth dipnet survey when we observed 13 unmarked Striped Newt larvae (10-20mm SVL) in the enclosures.

In total, we detected reproduction by released individuals (F0s) in five out of six enclosures (Table 3.4). In one of the low density enclosures, we detected one larval F1 in May (Table 3.4). No F1 individuals were detected again in any low density enclosures regardless of removal of marked individuals (Table 3.4).

We detected Striped Newt eggs in both medium density enclosures (Table 3.4). In the medium density enclosure with marked newts removed, we detected nine surviving paedotypic F1 individuals, eight of which had secondary sex characteristics (Table 3.4). We never detected F1 larvae in the medium density enclosure where marked individuals remained despite detection of eggs (Table 3.4).

In the high density enclosures, we detected eggs in one and larvae in both (Table 3.4). In the high density enclosure where marked newts were removed, we detected a maximum of seven F1 individuals. We found no surviving F1s in the high density enclosure where marked individuals remained.

Cormack-Jolly-Seber Model

The results from the CJS model indicated that apparent survival probability varied with both stocking density and release body size (SVL), but the estimated relationships were highly uncertain (Figure 3.4). The mean effect of body size at release on apparent survival probability was slightly positive, yet the 95% credible intervals broadly overlapped zero, and the probability of posterior direction was 76%, indicating moderate uncertainty (Table 3.5). Similarly, apparent survival probability appeared to decline with increasing stocking density, but this effect was also uncertain, with 95% credible intervals spanning negative to near-zero values (Table 3.5). The capture probabilities were low overall. There appeared to be a negative relationship between capture probability and water depth indicating that deeper water in enclosures reduced detection probability (Figure 3.4). The posterior estimates of variance among enclosures suggested moderate random effects of enclosure (Table 3.5). The results of the CJS model suggest survival was generally high but variable across enclosures, with weak evidence for density dependence and low detection that decreased with water depth.

Generalized Linear Model

The results of the Bayesian generalized linear model indicated that paedotypy was not strongly influenced by either stocking density or release body size (Figure 3.5). Both covariates had estimates with credible intervals overlapping zero (Table 3.6), providing little evidence for a consistent effect on the probability of remaining paedotypic. The Bayesian p-value for stocking density was 0.52, suggesting no support for a directional relationship between stocking density and paedotypy. For body size at release, the Bayesian p-value was higher (0.756), indicating that approximately 76% of the posterior samples suggested a negative effect.

Discussion

Our objective was to evaluate the success of captive-reared Striped Newts under experimental soft-release conditions, focusing on Seddon's (2010) first two criteria for assessing translocation success: survival of released individuals and reproduction by the release generation and their offspring. Our results demonstrate that captive-reared Striped Newts released into soft-release enclosures survived at a high rate and reproduced within their first year of release, with offspring capable of reaching sexual maturity in under a year when wetland hydroperiod is adequate. These outcomes met the initial criteria for translocation success outlined by Seddon (2010). We found only weak evidence for a negative effect of stocking density and a positive effect of size at release on newt survival. Given our limited sample size for each stocking density treatment, it is not surprising there was moderate to high uncertainty in our estimates. However, given the high posterior support for directional effects, it is unlikely that survival was unaffected by stocking density or body size at release. Navis (2025) also demonstrated positive effect of body size on captive-bred, larval Striped Newt survival in soft release enclosures. We found no evidence that body size or stocking density influenced the likelihood that a Striped Newt remained paedotypic. Our results differ from earlier studies by Navis (2025) who found that releasing Striped Newt larvae at a larger size substantially reduced the likelihood the animal would remain paedotypic. That worked suggested there was a size-dependent point at which the captive-rearing environment would trigger Striped Newts to develop into a terrestrial form subadult or adult. The difference between that early study and our study is likely attributable to improvements in captive rearing methods pioneered by Thomas et al. (in press) that promoted larvae to retain large gills and other larval traits late into larval development. Therefore, growing evidence suggests that releasing larger larval Striped Newts at intermediate stocking densities into soft-release enclosures can produce positive outcomes including rapid recruitment of breeding adults when wetland hydroperiod in adequate, though the latter outcome likely depends on larval captive husbandry prior to release.

Our survival estimates of newts released into soft-release enclosures are likely higher than would be realized using hard-release translocations. The use of soft-release enclosures likely contributed to early survival and breeding success by buffering against predation, allowing individuals to acclimate to wetland conditions, and maintaining sufficient local densities to ensure mating opportunities (Resende et al., 2021). While our results suggest promising survival outcomes, we caution against extrapolating these survival estimates to other landscapes or release strategies given variation in habitat conditions like hydroperiod and ecological pressures.

Successful reproduction of Striped Newts in our study occurred within a month of release and several F1 individuals matured sexually within the same year, demonstrating that captive-reared paedotypic adults can contribute viable offspring almost immediately after release. These findings are consistent with observations from wild populations (Johnson, 2002) and provide evidence for Seddon's (2010) second criterion: successful reproduction by the release generation and their offspring. Reproductive outcomes varied by stocking density and adult presence. The absence of surviving F1s at low densities, even after adult removal, may reflect positive density dependence (Allee effect), where insufficient numbers reduce the likelihood of successful reproduction or recruitment. The absence of surviving F1s in enclosures where larger stocked larvae and adults were allowed to remain after reproduction suggests that larger conspecifics may suppress juvenile persistence, likely through cannibalism or interference competition, a pattern that is well documented in other salamander species (Gabor, 1996; Polis & Myers, 1985; Walls, 1990). While very low stocking densities may risk reproductive failure due to Allee effects, very high densities may elevate risks of competition and cannibalism; therefore, we advocate for the use of intermediate stocking densities and the removal of the released cohort following detected reproduction to improve F1 recruitment.

The recruitment of paedotypic adults likely provides a key mechanism for rapid population growth in both wild and reintroduced Striped Newt populations (Dodd, 1993; Johnson, 2002; Navis, 2025). This accelerated recruitment within the first year (Denoël & Joly, 2001) may be especially important in translocation contexts to buffer against stochastic losses and support long-term viability in populations that have been extirpated or reduced to critically low numbers. In our study, paedotypy was common among survivors but showed no clear relationship with release body size or stocking density (Doyle & Whiteman, 2008). In addition to captive rearing husbandry, environmental conditions during our study may have affected the proportion of individuals that remained paedotypic. During our study period, the region experienced high precipitation that filled the wetland for at least 10 months, and the wetland reached a maximum water depth of 95 cm; long term hydrologic monitoring of the wetland has shown that the wetland typically dries down in early summer (Golladay et al., 2021). This extended inundation likely promoted paedotypy, as hypothesized by Whiteman (1994), who suggested wetland conditions like hydroperiod interact with genetic predisposition to dictate life-history pathways. Restoration actions that extend hydroperiod, such as upland thinning or woody vegetation removal (Golladay et al., 2021; Jones et al., 2018), may therefore facilitate paedotypy in restored wetlands and improve translocation outcomes (Dodd, 1993). Because paedotypy can provide an important buffer during the early stages of population establishment (Dodd, 1993), explicitly incorporating hydroperiod management into restoration and translocation strategies may be valuable for long-term management success.

Our study was focused on the performance of captive-bred and reared Striped Newts in wild conditions. Previous research has demonstrated that captive bred individuals tend to experience either genetic or performance deficits relative to their wild counterparts (Gross et al., 2024). These deficits are hypothesized to stem from inbreeding depression, artificial selection of maladaptive genes, and lack of exposure to predators and environmental conditions (Laikre et al., 2010; Teitelbaum et al., 2019; Tetzlaff et al., 2019; Turko et al., 2023). As a result, managers have traditionally been encouraged to prioritize the translocation of wild individuals to supplement populations instead of relying on captive stock. However, for rare and declining species with no proximate source populations, or where wild populations already exist in critically low numbers, like the Striped Newt, captive-bred individuals remain an essential resource. The moderately high survival rates observed in our study suggest that advances in husbandry practices and soft-release enclosures can assist in acclimatizing captive-bred Striped Newts, thereby increasing overall survival. It is currently unknown how survival rates of captive-bred individuals in our study compare directly to that of wild-born translocations. We encourage future releases to investigate the performance differences of wild captive-bred and wild translocated Striped Newts to guide future management decisions.

Some of our model estimates would have been improved if we had more individuals available for release. Our sample size was dictated by the number of individuals and life stages available at the time of the release, and our experimental design was adapted accordingly. Relatively small sample sizes and limited replication are common challenges in translocation projects, especially for cryptic and rare species with low detection probabilities. In our study, baseline detection probability was low despite the use of soft-release enclosure and declined further with increased water depth. Such imperfect detection can bias survival estimates in aquatic environments, reinforcing the need for robust monitoring frameworks that explicitly account for low detection in translocation assessments (Lyons et al., 2008). To address these limitations, we chose to analyze our data using Bayesian models. Bayesian inference can allow meaningful interpretation even under data-poor conditions by producing full posterior distributions and transparent measures of uncertainty (Ellison, 1996; Howes et al., 2010). We strongly recommend incorporating uncertainty into translocation assessments to strengthen their value for conservation decision-making as managers can evaluate risks and trade-offs based on probabilities rather than point estimates.

Species are disappearing worldwide at unprecedented rates (IUCN, 2023). Many species now face an extinction debt (Kuussaari et al., 2009), creating a narrow, but critical window in which proactive intervention can prevent irreversible loss (Semper-Pascual et al., 2018). Increased numbers of translocations over the past decades (Seddon et al., 2007), reflect this urgency, yet many projects have produced limited or uncertain results, and the drivers of success or failure remain unclear. Embedding an experimental component within translocations and applying adaptive management like this study can simultaneously accomplish management objectives and advance ecological understanding (Williams & Brown, 2012, 2018). Integrating adaptive management and Bayesian inference into future translocation efforts will provide a structured framework for confronting uncertainty allowing managers to base decisions on probabilistic outcomes and update strategies as new data accumulate (Folt et al., 2019).

The results of this study provide insights for improving amphibian translocation practices and guiding management decisions for Striped Newts. Our findings provide evidence of potential tradeoffs associated with stocking density. While low stocking densities may risk reproductive failure through Allee effects, high stocking densities may reduce survival and increase the likelihood of cannibalism. Adaptive management strategies, such as staged removal of adults following reproduction, may optimize survival and recruitment. Continued monitoring in subsequent seasons for returning newts and supplemental releases are likely necessary to support the establishment of a Striped Newt population at Ichauway. Future releases at Ichauway should prioritize a learning component and focus on addressing uncertainties regarding release performance between wild and captive newts and the factors that influence their survival and fecundity. We encourage managers to pair translocations with habitat restoration here necessary, to replicate experiments across landscapes to inform best practices, and continue long-term monitoring to build the comparative knowledge base needed to establish self-sustaining Striped Newt populations across their historic range.

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Tables

Table 3.1. Summary of stocking densities of Striped Newts for each soft-release enclosure and treatment, including the number of juveniles, adult females, and adult males.

			Adults		
Treatment	Enclosure ID	Juvenile	Female	Male	Total Newts
Low	1	5	2	2	9
Low	2	5	2	2	9
Medium	3	10	5	2	17
Medium	4	10	5	2	17
High	5	17	10	5	32
High	6	17	10	5	33

Table 3.2. Summary of post-release survival of Striped Newts in each soft-release enclosure and treatment. Values include stocking density at release, the number of individuals that survived to the end of the study, and corresponding survival percentages.

Treatment	Enclosure	Stocking Density	Number Survived	Post-Release Survival (%)
Low	1	9	7	77.8
Low	2	9	8	88.9
Medium	3	17	16	94.1
Medium	4	17	12	70.6
High	5	32	17	53.1
High	6	32	24	75

Table 3.3. Summary of Striped Newts released as gilled juveniles or gilled adults in each soft-release enclosure and treatment, and the percentage of individuals that remained gilled at the end of the study.

Treatment	Enclosure	Start Gilled	End Gilled	End Gilled (%)
Low	1	7	5	71.4
Low	2	9	6	66.7
Medium	3	16	14	87.5
Medium	4	14	10	71.4
High	5	32	17	53.1
High	6	30	17	56.7

Table 3.4. Summary of egg and F1 offspring detection of Striped Newts for each soft release enclosure and density treatment at a geographically wetland at the Jones Center at Ichauway in 2024.

Treatment	Enclosure	Eggs Detected	F1 larvae Detected	Conspefics Removed	F1s Survived
Low	1	No	No	Yes	No
Low	2	No	Yes	No	No
Medium	3	Yes	Yes	Yes	Yes
Medium	4	Yes	No	No	No
High	5	Yes	Yes	No	No
High	6	No	Yes	Yes	Yes

Table 3.5. Summary of parameter estimates from an open-population Cormack-Jolly-Seber model of survival and detection covariates for translocated Striped Newts in Baker County, Georgia, USA. Estimates in bold indicate parameters for which the Bayesian p-value (the proportion of posterior simulations in which the parameter estimate had the same sign the posterior mean) > 0.80.

Definition	Mean	95% CI		Bayesian p-value
Survival ~ SVL	0.185	-0.343	0.711	0.764
Survival ~ Density	**-0.867**	**-2.447**	**0.685**	**0.881**
Detection ~ Depth	**-0.106**	**-0.203**	**-0.006**	**0.981**
Enclosure random effect (SD)	**3.139**	**0.493**	**4.910**	**1.000**

Table 3.6. Summary of parameter estimates from a Bayesian generalized linear model of survival and detection covariates for translocated Striped Newts in Baker County, Georgia, USA.

Variable	Definition	Mean	95% CI		Bayesian p-value
beta1	Paedotypy ~ Density	-0.037	-1.300	1.190	0.521
beta2	Paedotypy ~ SVL	-0.200	-0.770	0.360	0.756

Figures

Figure 3.7. Soft-release enclosure with open top and mesh siding used for captive-reared Striped Newt larvae released at The Jones Center at Ichauway in Baker County, Georgia, USA.

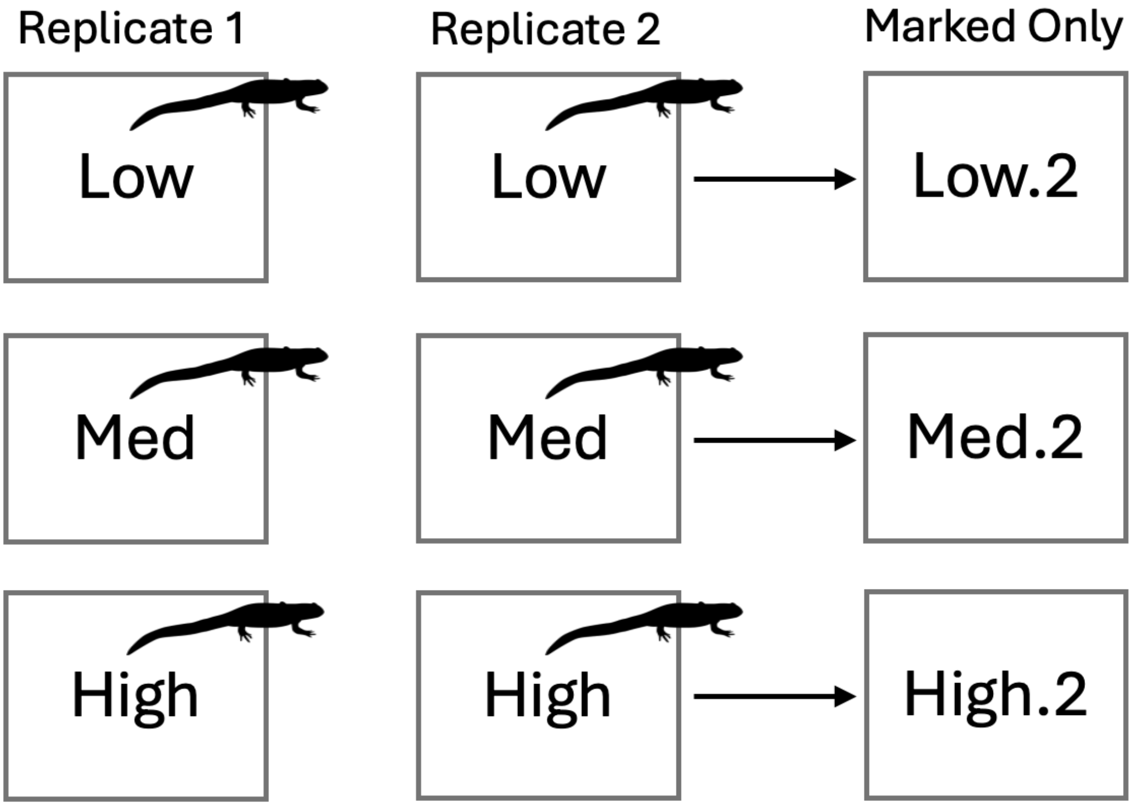

Figure 3.2. Diagram of soft-release enclosures following removal of marked Striped Newts in half of the replicates one month after reproduction was detected. Boxes labeled “Low,” “Medium,” and “High” represent the original release enclosures with their respective stocking density treatments, while “Low.2,” “Medium.2,” and “High.2” denote the new enclosures to which adults were transferred. Newt silhouettes indicate enclosures where marked newts were present at the end of the study.

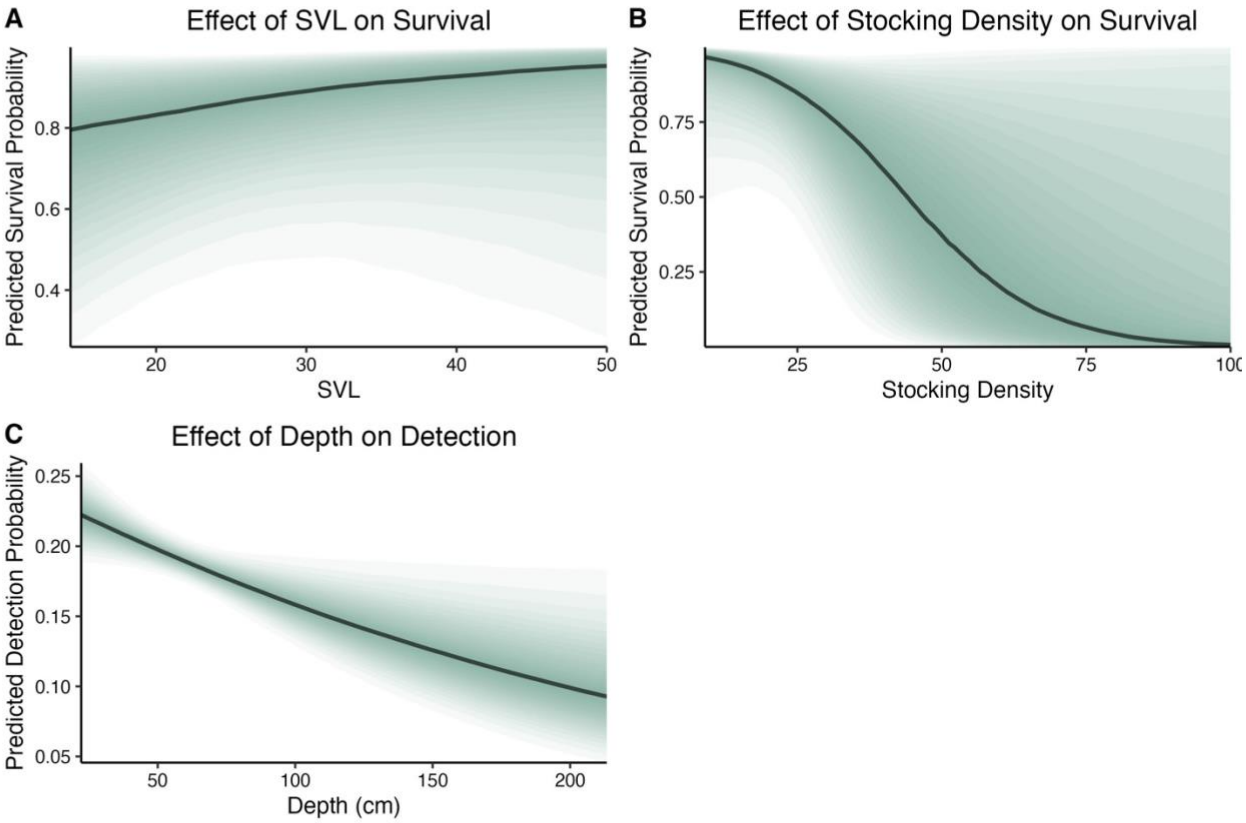

Figure 3.3. Predicted effect of initial body size (Release SVL) and stocking density on apparent survival probability and the predicted effect of maximum water depth in centimeters on detection probability based on posterior estimates from an open-population Cormack-Jolly-Seber model for captive-reared Striped Newts in soft-release enclosures at the Jones Center at Ichauway in Baker County, Georgia, USA. (A) Predicted effect of body size as snout–vent length (SVL)in millimeters at release on apparent survival probability. (B) Predicted effect of stocking density on apparent survival probability. (C) Predicted effect of effect of maximum water depth in centimeters on detection probability. Lines represent posterior means, and shaded ribbons show 95% (darkest) to 5% (lightest) credible intervals.

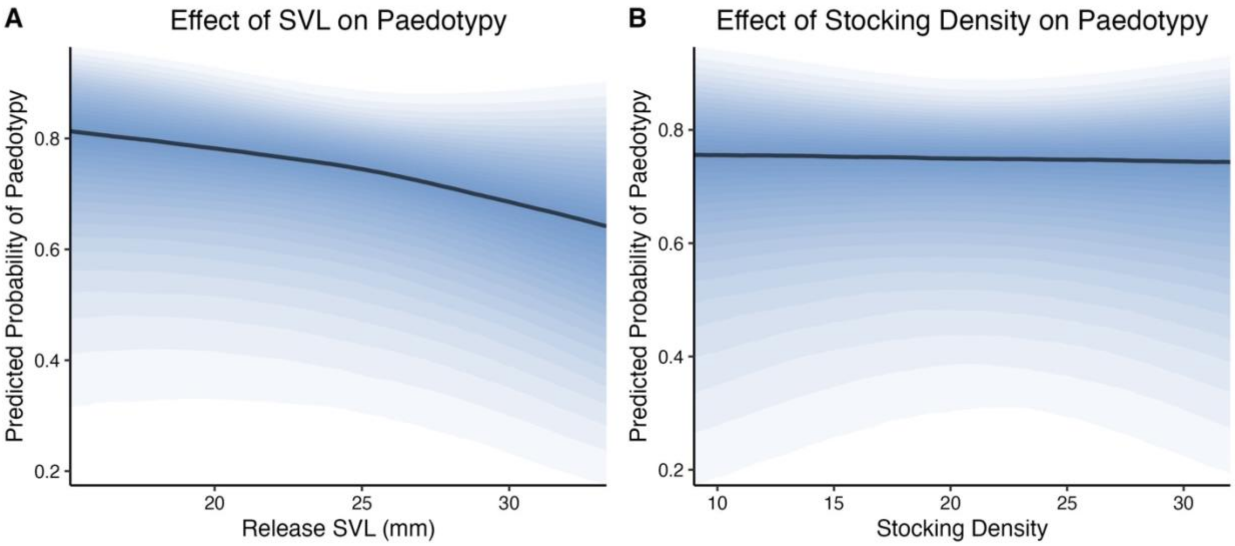

Figure 3.4. Predicted effect of initial body size (Release SVL) and stocking density on survival probability and probability of remaining paedotypic indviduals based on posterior estimates from a Bayesian generalized linear model for captive-reared Striped Newts in soft-release enclosures at the Jones Center at Ichauway in Baker County, Georgia, USA. (A) Predicted effect of body size as snout–vent length (SVL) in millimeters at release on the probability of retaining paedotypic traits. (B) Predicted effect of stocking density on the probability of a survived individual remaining paedotypic. Lines represent posterior means, and shaded ribbons show 95% (darkest) to 5% (lightest) credible intervals.

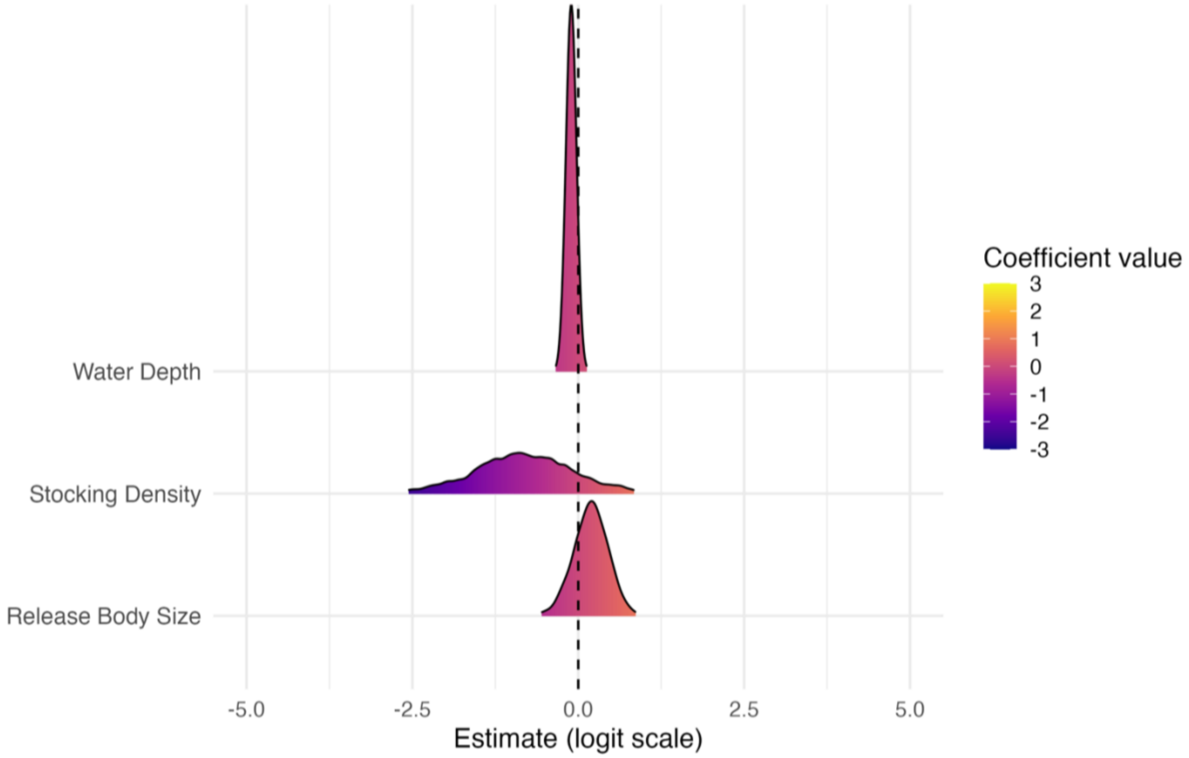

Figure 3.5. Posterior distributions for coefficients on detection and survival from an open-population Cormack-Jolly-Seber (CJS) model for Striped Newts in soft-release enclosures in Baker County, Georgia, USA. Water depth is the posterior distribution of estimates for the effect of maximum water depth on capture probability. Stocking density is the posterior distribution of estimates for the effect of stocking density on survival probability. Release body size is the posterior distribution of estimates for the effect of the body size at release measured as snout-to-vent length in millimeters on survival probability.

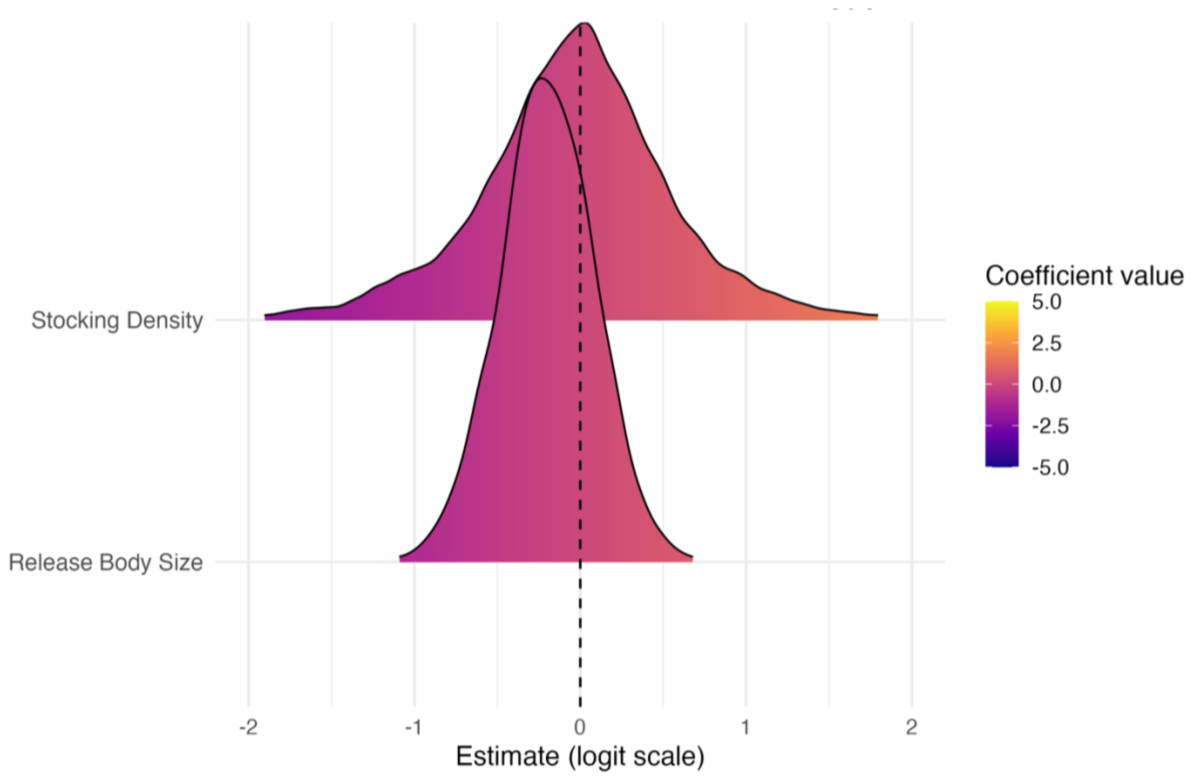

Figure 3.6. Posterior distributions for coefficients on the probability of a suriving individual being paedotypic at the end of the study from a Bayesian generalized linear model for Striped Newts in soft-release enclosures in Baker County, Georgia, USA. Stocking density is the posterior distribution of estimates for the effect of stocking density on paedotypy probability. Release body size is the posterior distribution of estimates for the effect of the body size at release measured as snout-to-vent length in millimeters on paedotypy probability.

CHAPTER 4

CONCLUSION

Modeling Amphibian To Wetland Conditions In Georgia

Our current findings suggest that wetlands conditions (canopy cover, hydroperiod, and distance to nearest occupied wetland) had variable but generally directional effects on amphibian occupancy across species. Although many parameter estimates had wide credible intervals overlapping zero, several species exhibited moderate to strong posterior support (Bayesian $p > 0.80$) for at least one wetland covariate. However, assessments of model convergence indicated poor mixing in some parameter so any inferences or conclusions drawn from these results must be qualified and considered provisional until resolved in future analysis. Our current results indicate that certain restoration actions like canopy thinning and prescribed fire may produce short-term benefits or transient community shifts, but that species responses differ depending on habitat requirements, disturbance tolerance, and landscape legacies. At the group level, our results showed evidence of trends consistent with known ecological patterns among amphibian taxa in the Southeastern Coastal Plain. Most salamanders (*Ambystoma, Eurycea, Notophthalmus*) showed negative effects of increasing hydroperiod, consistent with preference for ephemeral wetlands that reduce predation risk from fish (Semlitsch, 1980, 1987, 2000). Species-level responses were highly variable, reflecting diversity among amphibian life histories, dispersal capacities, and habitat specialization.

Our results suggested that landscape legacies, landscape size, historic and current land use, land management, and the current status of amphibian species within those landscapes has strong effects on wetland occupancy. The effect of landscape was particularly clear for our amphibian species of conservation concern. For example, Striped Newts were detected in only one wetland in one of the four landscapes. The species was last detected in the two other focal landscapes in 2006 and 2008 and there are no records of the species in the fourth landscape though that landscape is within the species' range. Gopher Frogs were detected on three of the focal landscapes but were abundant at multiple wetlands only at Ichauway, suggesting population status at each landscape strongly shapes the time it may take for species to respond to management. The rarity and isolation of Gopher Frog and Striped Newt populations suggest that habitat management alone may not be sufficient for species recovery and population supplementation or reintroduction via translocation or captive rearing will be needed in combination with restoration to improve relic or extirpated populations (Armstrong & Seddon, 2008; Ewen & Armstrong, 2007; Martin et al., 2025).

The inclusion of group-level pooling in our model likely enhanced some inference by allowing parameter estimates to draw information from closely related taxa, improving precision for data-limited species. Partial-pooling and hierarchical structure can be particularly valuable in amphibian community models where detection probabilities are low and sample sizes vary among species (Guzy et al., 2019; Kéry & Royle, 2016). However, pooling at the genus level can also mask meaningful ecological differences when taxa within groups differ in habitat use or life history, despite being closely related. For instance, while *Hyla avivoca* and *Hyla squirrela* are taxonomically related species, yet they differ substantially in habitat specialization and sensitivity to hydrologic change. Thus, while group-level pooling can improve model stability, future modeling efforts may benefit from grouping by ecological guild rather than taxonomy (Dorazio & Connor, 2014).

Inference from this study was limited by inconsistent monitoring effort, uneven application of restoration actions, and a relatively small sample size of wetlands compared to the complexity of the questions addressed. Our analysis could not isolate the effect of individual restoration actions due to limited replication and variation among treatment intensity. While our model attempts to capture some of the complexity inherent in restoration systems by using canopy cover and hydroperiod as a measure of desirable wetland conditions, its explanatory power was ultimately limited by the scope and design of the data. However, our results highlight the need for quantitative metrics of restoration (e.g., basal area removed, percent canopy cover thinned, confirmation and extent of wetland basin burned) and long-term monitoring to capture delayed amphibian community responses, especially for rare taxa or those with episodic recruitment, so that any negative emerging effects can be identified or additional management actions can be incorporated to improve decisions and better meet management long-term objectives.

This study illustrates the potential for adaptive management to link management actions to measurable learning outcomes (Williams & Brown, 2018). By evaluating monitoring data with an integrated Bayesian occupancy model, we demonstrate that restoration can serve both as a management action and an opportunity to learn and inform future decisions. However, this process depends on the abundance and variation of long-term, consistent monitoring across relevant temporal and spatial scales. Without relevant post-restoration monitoring and a structured experimental design, it is difficult to distinguish short-term variability from true management effects. Future restoration efforts must therefore incorporate a clearly defined learning component prior to implementation, emphasizing hypothesis-driven management, standardized protocols, quantitative metrics, and iterative evaluation to ensure actions advance conservation outcomes and ecological understanding (Williams & Brown, 2012).

Experimental Soft-Release Translocation of Striped Newts at Ichauway

Captive-reared Striped Newts released into soft-release enclosures within a natural wetland survived at a high rate and reproduced within their first year of release, with offspring capable of reaching sexual maturity in under a year. These outcomes met the initial criteria for translocation success outlined by Seddon (1999). We found only weak evidence for a negative effect of stocking density and a positive effect of size at release on newt survival. Given our limited sample size for each stocking density treatment, it is not surprising there was moderate to high uncertainty in our estimates. However, given the high posterior support for directional effects, it is unlikely that survival was unaffected by stocking density or body size at release. Navis (2025) also demonstrated positive effect of body size on captive-bred, larval Striped Newt survival in soft release enclosures. We found no evidence that body size or stocking density impacted the likelihood a Striped Newt would remain paedotypic.

Our results differ from earlier studies by Navis (2025) who found that releasing Striped Newt larvae at a larger size substantially reduced the likelihood the animal would remain paedotypic. That worked suggested there was a size-dependent point at which the captive-rearing environment would trigger Striped Newts to develop into a terrestrial form subadult or adult. The difference between that early study and our study is likely attributable to improvements in captive rearing methods pioneered by C. Thomas (Thomas et al. in press) that promoted larvae to retain large gills and other larval traits late into larval development. Therefore, growing evidence suggests that releasing larger larval Striped Newts at intermediate stocking densities into soft-release enclosures can produce positive outcomes including rapid recruitment of breeding adults though the latter outcome likely depends on larval captive husbandry prior to release.

In our study, paedotypy was common among survivors but showed no clear relationship with release body size or stocking density (Doyle & Whiteman, 2008). The recruitment of paedotypic adults likely provides a key mechanism for rapid population growth in both wild and reintroduced Striped Newt populations (Dodd, 1993; Johnson, 2002). This accelerated recruitment within the first year (Denoël & Joly, 2001) may be especially important in translocation contexts to buffer against stochastic losses and support long-term viability in populations that have been extirpated or reduced to critically low numbers. Extended inundation during our study period likely promoted paedotypy, as hypothesized by Whiteman (1994), who suggested wetland conditions like hydroperiod interact with genetic predisposition to dictate life-history pathways. Restoration actions that extend hydroperiod, such as upland thinning or woody vegetation removal (Golladay et al., 2021; Jones et al., 2018), may therefore facilitate paedotypy in restored wetlands and improve translocation outcomes (Dodd, 1993). Since Paedotypy can provide an important buffer during the early stages of population establishment (Dodd, 1993), explicitly incorporating hydroperiod management into restoration and translocation strategies may be valuable for long-term management success.

Our sample size was dictated by the number of individuals and life stages available at the time of the release and our experimental design was adapted accordingly. Relatively small sample sizes and limited replication are common challenges in translocation projects, especially for cryptic and rare species with low detection probabilities. In our study, baseline detection probability was very low despite the use of soft-release enclosures and declined further with increased water depth. Such imperfect detection can bias survival estimates in aquatic environments, reinforcing the need for robust monitoring frameworks that explicitly account for low detection in translocation assessments (Lyons et al., 2008). To address these limitations, we chose to analyze our data using Bayesian models. Bayesian inference can allow meaningful interpretation even under data-poor conditions by producing full posterior distributions and transparent measures of uncertainty (Ellison, 1996; Howes et al., 2010). We strongly recommend incorporating uncertainty into translocation assessments to strengthen their value for conservation decision-making as managers can evaluate risks and trade-offs based on probabilities rather than point estimates.

The results of this study provide insights for improving amphibian translocation practices and guiding management decisions for Striped Newts. Our findings provide evidence of potential tradeoffs associated with stocking density. While very low stocking densities may risk reproductive failure through Allee effects, high stocking densities may reduce survival and increase the likelihood of cannibalism. Adaptive management strategies, such as staged removal of adults following reproduction, may optimize survival and recruitment. We encourage managers to pair translocations with habitat restoration where necessary, to replicate experiments across landscapes to inform best practices, and continue long-term monitoring to build the comparative knowledge base needed to establish self-sustaining Striped Newt populations across their historic range.

We advocate for the formal adoption of an adaptive management framework for ongoing wetland restoration and amphibian translocation projects by land and wildlife management agencies or other organizations to improve learning from ongoing management and improve future decision making. Our study illustrates the potential for such an adaptive management program to link management actions to measurable learning outcomes provided there is adequate design and execution of management actions and subsequent monitoring (Williams & Brown, 2018). Ongoing and future restoration and translocation efforts clearly serve as actions and opportunities to inform future management decisions. However, this process depends on the thoughtful planning and distribution of actions, consistent monitoring across relevant temporal and spatial scales, and the use of robust models that can account for imperfect detection and incorporate multiple monitoring methods. For rare and threatened species, high uncertainty and delays in learning whether actions are working can prove particularly costly with the loss of few remaining populations. Restoration and translocation efforts must incorporate and commit resources to clearly defined learning components prior to implementation, emphasizing hypothesis-driven management, standardized protocols, multiple methods, and iterative evaluation to ensure actions advance conservation outcomes and ecological understanding (Williams & Brown, 2012).

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APPENDICES

Appendix 2.1. Total numbers of each taxon detected at 17 wetlands within Alapaha River Wildlife Management Area from February 2019 to July 2024. Values represent the number of unique detection events, not the number of unique animals detected.

Site		Species	# Wetlands	# Observations
Alapaha River WMA	Anura	*Acris gryllus*	17	1597
		Anaxyrus fowleri	1	1
		Anaxyrus quercicus	16	178
		Anaxyrus terrestris	17	84
		Gastrophryne carolinensis	17	270
		Hyla avivoca	1	2
		Hyla chrysoscelis	16	117
		Hyla cinerea	17	237
		Hyla femoralis	17	677
		Hyla gratiosa	17	359
		Hyla squirella	14	62
		Pseudacris crucifer	17	1384
		Pseudacris feriarum	12	22
		Pseudacris nigrita	17	400
		Pseudacris ocularis	17	1907
		Pseudacris ornata	17	721
		Rana capito	7	28
		Rana catesbeiana	16	432
		Rana clamitans	17	332
		Rana grylio	9	17
		Rana sphenocephala	17	1849
		Scaphiopus holbrookii	13	79
	Caudata	*Ambystoma talpoideum*	1	2
		Ambystoma tigrinum	14	76
		Eurycea quadridigitata	10	46
		Notophthalmus perstriatus	1	19
		Notophthalmus viridescens	8	12

Appendix 2.2. Total numbers of each taxon detected at 6 wetlands within Cabin Bluff from May 2022 to June 2024. Values represent the number of unique detection events, not the number of unique animals detected.

Site		Species	# Wetlands	# Observations
Cabin Bluff	Anura	*Acris gryllus*	6	213
		Anaxyrus quercicus	5	17
		Anaxyrus terrestris	4	16
		Gastrophryne carolinensis	3	7
		Hyla chrysoscelis	1	1
		Hyla cinerea	2	8
		Hyla femoralis	6	77
		Hyla gratiosa	2	3
		Hyla squirella	3	5
		Pseudacris crucifer	6	54
		Pseudacris nigrita	3	5
		Pseudacris ocularis	6	242
		Pseudacris ornata	1	1
		Rana catesbeiana	1	1
		Rana clamitans	2	10
		Rana grylio	3	31
		Rana sphenocephala	6	159
		Scaphiopus holbrookii	4	7

Appendix 2.3. Total numbers of each taxon detected at 14 wetlands within Ceylon Wildlife Management Area from April 2022 to July 2024. Values represent the number of unique detection events, not the number of unique animals detected.

Site		Species	# Wetlands	# Observations
Ceylon WMA	Anura	*Acris gryllus*	14	582
		Anaxyrus quercicus	10	38
		Anaxyrus terrestris	6	32
		Gastrophryne carolinensis	8	40
		Hyla chrysoscelis	7	34
		Hyla cinerea	11	98
		Hyla femoralis	13	274
		Hyla gratiosa	11	103
		Hyla squirella	9	20
		Pseudacris crucifer	13	186
		Pseudacris nigrita	2	4
		Pseudacris ocularis	13	411
		Pseudacris ornata	1	2
		Rana capito	3	17
		Rana catesbeiana	5	7
		Rana clamitans	11	88
		Rana grylio	12	266
		Rana sphenocephala	14	558
		Scaphiopus holbrookii	2	2
	Caudata			
		Notophthalmus viridescens	2	5

Appendix 2.4. Total numbers of each taxon detected at 13 wetlands within Ichauway from February 2023 to July 2024. Values represent the number of unique detection events, not the number of unique animals detected.

Site		Species	# Wetlands	# Observations
Jones Center at Ichauway	Anura	*Acris gryllus*	12	747
		Anaxyrus terrestris	9	44
		Gastrophryne carolinensis	9	97
		Hyla chrysoscelis	5	23
		Hyla cinerea	8	159
		Hyla femoralis	12	198
		Hyla gratiosa	12	250
		Hyla squirella	12	136
		Pseudacris crucifer	9	150
		Pseudacris feriarum	2	3
		Pseudacris nigrita	12	576
		Pseudacris ocularis	4	10
		Pseudacris ornata	12	265
		Rana capito	10	202
		Rana catesbeiana	9	83
		Rana clamitans	7	32
		Rana grylio	1	1
		Rana sphenocephala	12	468
		Scaphiopus holbrookii	3	16
	Caudata			
		Ambystoma talpoideum	6	10
		Ambystoma tigrinum	7	17
		Eurycea quadridigitata	8	25
		Notophthalmus viridescens	4	12
		Pseudobranchus striatus	2	6

Appendix 2.5. Total numbers of each taxon detected at 5 wetlands within Townsend Wildlife Management Area from January 2021 to July 2024. Values represent the number of unique detection events, not the number of unique animals detected.

Site		Species	# Wetlands	# Observations
Townsend WMA	Anura	*Acris gryllus*	5	190
		Anaxyrus quercicus	4	28
		Anaxyrus terrestris	4	27
		Gastrophryne carolinensis	2	7
		Hyla chrysoscelis	1	1
		Hyla cinerea	2	7
		Hyla femoralis	5	88
		Hyla gratiosa	2	5
		Hyla squirella	1	2
		Pseudacris crucifer	5	135
		Pseudacris nigrita	4	120
		Pseudacris ocularis	5	335
		Pseudacris ornata	3	8
		Rana catesbeiana	2	3
		Rana clamitans	2	38
		Rana grylio	1	32
		Rana sphenocephala	5	177
	Caudata			
		Eurycea quadridigitata	2	5

Appendix 2.6. Parameters flagged for convergence and poor mixing issues in occupancy model. Entries include R-hat values, effective sample sizes (n.eff), and whether each parameter exceeded convergence thresholds (R-hat > 1.01 or n.eff < 400).

Parameter	R-hat	n.eff	Bad R-hat	Low n.eff
alpha0[4]	1.018	551	TRUE	FALSE
alpha0[5]	1.031	84	TRUE	TRUE
alpha0[6]	1.016	216	TRUE	TRUE
alpha0[7]	1.021	164	TRUE	TRUE
alpha0[8]	1.019	136	TRUE	TRUE
alpha0[10]	1.046	66	TRUE	TRUE
alpha0[13]	1.043	57	TRUE	TRUE
alpha0[14]	1.018	114	TRUE	TRUE
alpha0[15]	1.013	156	TRUE	TRUE
alpha0[16]	1.010	218	TRUE	TRUE
alpha0[18]	1.018	198	TRUE	TRUE
alpha0[20]	1.020	129	TRUE	TRUE
alpha0[21]	1.040	71	TRUE	TRUE
alpha0[22]	1.012	172	TRUE	TRUE
alpha0[24]	1.020	139	TRUE	TRUE
alpha0[26]	1.025	85	TRUE	TRUE
alpha0[27]	1.043	54	TRUE	TRUE
alpha.canopy[5]	1.022	282	TRUE	TRUE
alpha.dist[3]	1.011	191	TRUE	TRUE
alpha.dist[6]	1.015	253	TRUE	TRUE
alpha.dist[8]	1.011	835	TRUE	FALSE
alpha.dist[15]	1.011	1049	TRUE	FALSE
alpha.dist[18]	1.017	159	TRUE	TRUE
alpha.hydro[5]	1.014	211	TRUE	TRUE
alpha.hydro[8]	1.017	123	TRUE	TRUE
alpha.hydro[18]	1.026	212	TRUE	TRUE
alpha.landscape[4,1]	1.014	1463	TRUE	FALSE
alpha.landscape[6,1]	1.017	147	TRUE	TRUE
alpha.landscape[10,1]	1.038	88	TRUE	TRUE
alpha.landscape[12,1]	1.011	1375	TRUE	FALSE
alpha.landscape[13,1]	1.023	99	TRUE	TRUE
alpha.landscape[14,1]	1.017	119	TRUE	TRUE
alpha.landscape[15,1]	1.018	114	TRUE	TRUE
alpha.landscape[16,1]	1.015	157	TRUE	TRUE

Parameter	R-hat	n.eff	Bad R-hat	Low n.eff
alpha.landscape[18,1]	1.014	218	TRUE	TRUE
alpha.landscape[20,1]	1.014	203	TRUE	TRUE
alpha.landscape[24,1]	1.018	147	TRUE	TRUE
alpha.landscape[26,1]	1.017	120	TRUE	TRUE
alpha.landscape[27,1]	1.042	56	TRUE	TRUE
alpha.landscape[4,2]	1.013	395	TRUE	TRUE
alpha.landscape[7,2]	1.021	143	TRUE	TRUE
alpha.landscape[10,2]	1.019	281	TRUE	TRUE
alpha.landscape[13,2]	1.028	83	TRUE	TRUE
alpha.landscape[16,2]	1.013	157	TRUE	TRUE
alpha.landscape[22,2]	1.015	139	TRUE	TRUE
alpha.landscape[24,2]	1.019	167	TRUE	TRUE
alpha.landscape[26,2]	1.021	96	TRUE	TRUE
alpha.landscape[27,2]	1.013	169	TRUE	TRUE
alpha.landscape[2,3]	1.017	154	TRUE	TRUE
alpha.landscape[5,3]	1.011	241	TRUE	TRUE
alpha.landscape[7,3]	1.011	242	TRUE	TRUE
alpha.landscape[8,3]	1.017	130	TRUE	TRUE
alpha.landscape[13,3]	1.010	308	TRUE	TRUE
alpha.landscape[21,3]	1.013	181	TRUE	TRUE
alpha.landscape[26,3]	1.010	190	TRUE	TRUE
alpha.landscape[27,3]	1.025	90	TRUE	TRUE
mu.alpha0[4]	1.021	164	TRUE	TRUE
mu.alpha0[5]	1.019	136	TRUE	TRUE
mu.alpha0[7]	1.010	218	TRUE	TRUE
mu.alpha0[8]	1.020	155	TRUE	TRUE
mu.alpha0[9]	1.012	172	TRUE	TRUE
mu.alpha0[10]	1.020	139	TRUE	TRUE
mu.alpha.dist[5]	1.011	835	TRUE	FALSE
mu.alpha.hydro[5]	1.017	123	TRUE	TRUE
beta0.dip[1]	1.019	200	TRUE	TRUE
beta0.dip[7]	1.021	250	TRUE	TRUE
beta0.dip[8]	1.022	93	TRUE	TRUE
beta0.dip[11]	1.046	49	TRUE	TRUE
beta0.dip[12]	1.014	159	TRUE	TRUE
beta0.dip[14]	1.012	164	TRUE	TRUE
beta0.dip[15]	1.040	88	TRUE	TRUE
beta0.dip[18]	1.015	201	TRUE	TRUE
beta0.dip[20]	1.039	74	TRUE	TRUE

Parameter	R-hat	n.eff	Bad R-hat	Low n.eff
beta0.dip[23]	1.012	196	TRUE	TRUE
beta0.dip[25]	1.021	132	TRUE	TRUE
beta0.dip[26]	1.027	101	TRUE	TRUE
beta.mon.dip[20,1]	1.029	127	TRUE	TRUE
beta.mon.dip[20,2]	1.031	136	TRUE	TRUE
beta.mon.dip[18,3]	1.011	231	TRUE	TRUE
beta.mon.dip[20,3]	1.029	138	TRUE	TRUE
beta.mon.dip[26,3]	1.011	274	TRUE	TRUE
beta.mon.dip[7,4]	1.014	182	TRUE	TRUE
beta.mon.dip[20,4]	1.029	157	TRUE	TRUE
beta.mon.dip[7,5]	1.019	118	TRUE	TRUE
beta.mon.dip[15,5]	1.011	190	TRUE	TRUE
beta.mon.dip[20,5]	1.024	129	TRUE	TRUE
beta.mon.dip[26,5]	1.010	260	TRUE	TRUE
beta.mon.dip[26,6]	1.010	261	TRUE	TRUE
beta.mon.dip[7,7]	1.013	153	TRUE	TRUE
beta.mon.dip[15,7]	1.011	180	TRUE	TRUE
beta.mon.dip[26,7]	1.010	240	TRUE	TRUE
beta.yr.dip[1,1]	1.022	225	TRUE	TRUE
beta.yr.dip[11,1]	1.043	53	TRUE	TRUE
beta.yr.dip[12,1]	1.011	182	TRUE	TRUE
beta.yr.dip[18,1]	1.013	431	TRUE	FALSE
beta.yr.dip[19,1]	1.014	211	TRUE	TRUE
beta.yr.dip[20,1]	1.040	57	TRUE	TRUE
beta.yr.dip[23,1]	1.011	237	TRUE	TRUE
beta.yr.dip[26,1]	1.018	122	TRUE	TRUE
beta.yr.dip[1,2]	1.015	185	TRUE	TRUE
beta.yr.dip[19,2]	1.011	270	TRUE	TRUE
beta.yr.dip[20,2]	1.014	149	TRUE	TRUE
beta.yr.dip[26,2]	1.016	128	TRUE	TRUE
beta.yr.dip[1,3]	1.026	198	TRUE	TRUE
beta.yr.dip[11,3]	1.043	52	TRUE	TRUE
beta.yr.dip[12,3]	1.014	140	TRUE	TRUE
beta.yr.dip[15,3]	1.018	151	TRUE	TRUE
beta.yr.dip[18,3]	1.011	382	TRUE	TRUE
beta.yr.dip[19,3]	1.015	201	TRUE	TRUE
beta.yr.dip[20,3]	1.039	56	TRUE	TRUE
beta.yr.dip[26,3]	1.021	104	TRUE	TRUE
beta.yr.dip[1,4]	1.026	181	TRUE	TRUE

Parameter	R-hat	n.eff	Bad R-hat	Low n.eff
beta.yr.dip[11,4]	1.037	61	TRUE	TRUE
beta.yr.dip[18,4]	1.017	189	TRUE	TRUE
beta.yr.dip[19,4]	1.017	180	TRUE	TRUE
beta.yr.dip[20,4]	1.038	58	TRUE	TRUE
beta.yr.dip[23,4]	1.014	183	TRUE	TRUE
beta.yr.dip[26,4]	1.018	121	TRUE	TRUE
beta.yr.dip[1,5]	1.024	208	TRUE	TRUE
beta.yr.dip[11,5]	1.033	68	TRUE	TRUE
beta.yr.dip[19,5]	1.017	164	TRUE	TRUE
beta.yr.dip[20,5]	1.036	61	TRUE	TRUE
beta.yr.dip[26,5]	1.019	117	TRUE	TRUE
beta.yr.dip[1,6]	1.028	168	TRUE	TRUE
beta.yr.dip[11,6]	1.043	51	TRUE	TRUE
beta.yr.dip[12,6]	1.012	166	TRUE	TRUE
beta.yr.dip[15,6]	1.026	111	TRUE	TRUE
beta.yr.dip[18,6]	1.015	296	TRUE	TRUE
beta.yr.dip[19,6]	1.018	161	TRUE	TRUE
beta.yr.dip[20,6]	1.044	51	TRUE	TRUE
beta.yr.dip[23,6]	1.011	225	TRUE	TRUE
beta.yr.dip[24,6]	1.011	200	TRUE	TRUE
beta.yr.dip[25,6]	1.015	149	TRUE	TRUE
beta.yr.dip[26,6]	1.017	129	TRUE	TRUE