MODELING OCCUPANCY AND HABITAT SUITABILITY TO GUIDE MANAGEMENT FOR THE GOPHER FROG (RANA CAPITO) IN SOUTH GEORGIA

by

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(Under the Direction of Jeffrey Hepinstall-Cymerman and John Maerz)

ABSTRACT

The Gopher frog (*Rana capito*), a species of concern in Georgia, has suffered population declines corresponding with the loss and alteration of southeastern Longleaf pine (*Pinus palustris*) ecosystems. Identifying habitat associations and remaining suitable habitat for the Gopher frog are essential first steps for implementing effective conservation management to sustain the species. In this study, I investigated Gopher frog and anuran occupancy among ponds within the Alapaha River Wildlife Management Area (ARWMA) using automated recording devices, dipnetting surveys, and egg mass surveys. I modeled detection rates and occupancy for the Gopher frog and a suite of winter-breeding anurans as a function of hydroperiod and canopy cover. I tested a technique to evaluate wetland hydroperiods of herbaceous and forested wetlands at ARWMA using a data set developed from Landsat imagery, and I developed a habitat suitability model that uses wetland and upland habitat attributes to identify potential breeding ponds for Gopher frogs at ARWMA.

INDEX WORDS: Pond-breeding amphibian; occupancy model; Gopher frog; habitat

suitability; hydroperiod; wetland; longleaf pine; vocal anuran;

canopy cover

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DEDICATION

How we spend our days is, of course, how we spend our lives.

— Annie Dillard

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction

Habitat loss is the single greatest threat to biodiversity worldwide (Brooks et al., 2002; Hanski, 2005; Cushman, 2006; Quesnelle, Fahrig, & Lindsay, 2013; Haddad et al., 2015; Newbold et al., 2015). Fragmentation of wildlife habitats compounds the threat to biodiversity, reducing the amount and quality of remaining habitat, isolating populations, and introducing new threats such as roads and increased vulnerability to predation (Fahrig, 2001; Haddad et al., 2015). Over 83% of the Earth's ice-free land area has been modified by humans, and, as natural ecosystems and habitats are reduced, wildlife populations experience increased stress and declines (Vitousek, Mooney, Lubchenco, & Melillo, 1997; Fahrig, 2001; Sanderson et al., 2002). Without human intervention to improve and restore degraded habitats, many populations will continue to decline, leading to local extinctions of sensitive species (Vitousek et al., 1997; Perring et al., 2015).

Once dominant ecosystems across the southeastern United States, today, pine-savannas such as the longleaf pine (*Pinus palustris*)-wiregrass (*Aristida* spp.) ecosystem have been reduced to less than 3-5% of their historic acreage (Peet & Allard, 1993; Noss, LaRoe, & Scott, 1995; Van Lear, Carroll, Kapeluck, & Johnson, 2005; USDA-NRCS, 2016; Peet, Platt, & Costanza, 2018). Pine savanna-associated forest, wetland, and

grassland communities support an incredible diversity of flora and fauna, including many species that can be found only within longleaf pine communities in the southeastern U.S. (Jackson & Milstrey, 1989; Outcalt, 2000; Earley, 2004; Brockway, 2005). Decades of timber harvest followed by land use transitions towards agriculture, plantation forestry, and industrial and residential development reduced and fragmented these longleaf pine savanna communities (Ware, Frost, & Doerr, 1993). Even lands which were not directly converted still bore the attendant costs of nearby land use conversion. The terrestrial and wetland habitats within the pine savannas were shaped and maintained by fire for millennia, but fire suppression became the new regime, and hundreds of thousands of acres of land across the southeastern U.S. saw a key natural disturbance largely removed from landscapes (Pyne, 1982; Earley, 2004; Frost, 2007). The longleaf pine ecosystem is one of the most threatened ecosystems in the world and is home to 29 federally listed species and many more that have been proposed to receive federal protection under the Endangered Species Act (Frost, 2007; USDA-NRCS, 2016).

Embedded within pine savannas is a diversity of wetland types, from small emergent or forested depression wetlands to extensive wet prairies, some of which are home to unique amphibian species (Dodd, 1992; Tiner, 2003; Erwin, Chandler, Palis, Gorman, & Haas, 2016). There are several pond-breeding amphibian species which are of conservation interest due to reported declines associated with the loss of their pine savanna habitats (Calhoun et al., 2015; Chandler, Rypel, Jiao, Haas, & Gorman, 2016). Little consideration or legal protection is afforded to many of the wetlands which are often critical habitat for pond breeding amphibians, and, since the beginning of the 18th century, 50% to 87% of wetlands in the southeastern U.S. have been drained or altered,

primarily for conversion to agriculture and plantation forestry (Fonseca et al., 2013; Lane & D'Amico, 2016; Stuber, Kirkman, Hepinstall-Cymerman, & Martin, 2016; Evans et al., 2017; Golden et al., 2017). Altering the hydrology of wetlands through modifications to wetlands and their adjacent terrestrial buffers can fundamentally alter wetland functions and associated communities (Snodgrass, Komoroski, Jr, & Burger, 2000; McCauley, Anteau, Post van der Burg, & Wiltermuth, 2015; Stuber et al., 2016). These wetlands are critical habitat for many amphibians within the pine savanna ecosystems.

For example, Gopher frogs (Rana capito) rely on ephemeral to semipermanent wetlands within pine savannas for breeding and open pine savanna uplands with Gopher tortoise burrows, small mammal burrows, or stump holes for terrestrial refuges (Franz, 1986; Jackson & Milstrey, 1989; Godley, 1992). First described in the 1950s, the Gopher frog (Rana capito) is a species nearly restricted to the Gulf and Atlantic Coastal Plain and the pine savanna communities of the southeastern U.S., with only two isolated populations ever recorded outside of this range (Redmond & Scott, 1996; Palis & Fischer, 1997; Hammerson & Jensen, 2004). Genetic studies of R. capito provide evidence for three distinct population segments of the Gopher frog throughout its range, with mitochondrial DNA delineating boundaries between a Coastal Plain Lineage northwest of the Sewanee River Basin and two Peninsular lineages (Richter et al., 2014). Though Gopher frog populations from the Peninsular Florida lineages appear stable (over 100 populations), the number of extant Coastal Plain lineage populations has declined substantially across much of northern Florida, Alabama, Georgia, South Carolina, and North Carolina (U.S. Fish and Wildlife Service, 1991; Jensen & Richter, 2005; Richter et al., 2014). As a result, the Gopher frog is IUCN listed as near threatened (Hammerson &

Jensen, 2004) and is a candidate species for federal protection. Gopher frog population declines are directly linked to both the extensive loss of pine savanna habitats and the degradation of remaining wetlands and uplands (Hefner & Brown, 1984; Franz, 1986; U.S. Fish and Wildlife Service, 1991).

Within Georgia, a number of conservation strategies have been developed to recover rare and threatened wildlife populations and are currently being used in Georgia to target several pine savanna ecosystem associates including the Gopher frog. These include activities such as captive breeding and captive rearing, reintroduction, and population supplementation; intensive monitoring and adaptive management programs; and habitat and ecosystem restoration practices. These activities are hindered by a number of factors, including limited data on the status of most remnant populations and habitat models to identify priority sites for acquisition, habitat restoration, and population augmentation or reintroduction. Specifically, it is important that we understand which habitat attributes are most important to population persistence and what factors currently limit Gopher frog occupancy and population growth within managed landscapes. Current distribution models for the Gopher frog available for Georgia (USGS Georgia GAP Analysis Program) (Kramer et al., 2003) and the region (USGS SEGAP Analysis Program) are useful in identifying potential priority conservation areas, but they are too coarse to inform management actions within these or established conservation areas. A finer-scale approach that considers the spatial configuration of habitat components within identified areas is needed for predicting networks of upland and wetland habitat that may sustain local Gopher frog populations. By evaluating wetlands and uplands where Gopher frogs are known to be persisting in Georgia from 2000 to the present, and by considering

both local- and landscape-level habitat characteristics of those localities, we can develop more fine-scale habitat models to inform specific, site-based actions.

Study Overview

Rigorous monitoring programs for Gopher frogs have identified fewer than twelve extant breeding populations in Georgia (Georgia Department of Natural Resources Unpublished data; Jensen & Richter, 2005; Maerz & Terrell, 2016), and the species exhibits several characteristics which may identify it as a high-risk for local extinctions: small population sizes, low reproductive rates, and high inbreeding potential (Semlitsch, Gibbons, & Tuberville, 1995). The state identifies the Gopher frog as "rare" and a species of greatest conservation need (SGCN) in its State Wildlife Action Plan (SWAP) (Georgia Department of Natural Resources Wildlife Resources Division, 2015). In 2013, a Gopher frog was detected in Irwin County, Georgia. A dispersing frog was found in a pitfall trap on the northeastern section of a privately-owned property (Georgia Department of Natural Resources Unpublished data). This 2,780-ha property was eventually sold to the state and established as the Alapaha River Wildlife Management Area (ARWMA; Alapaha) in the fall of 2016. The property was purchased for its conservation value for a number of threatened and endangered species, and, along with providing recreational opportunities for hunting, fishing, hiking, and wildlife viewing, the Wildlife Resources Division of Georgia DNR is committed to managing the property for those species (Georgia Department of Natural Resources, 2017). Interest in restoring the Gopher frog population at ARWMA motivated us to conduct wetland surveys to learn more about the amphibian communities within ARWMA and to model Gopher frog occupancy on the

site. Moreover, we aimed to model habitat suitability of apparently stable, extant Gopher frog populations across Georgia and then project that suitability model on to ARWMA to evaluate current wetland suitability and specific management actions that could improve available Gopher frog habitat and population persistence on the site. In addition, by modeling Gopher frog habitat at known sites throughout Georgia, we can refine our understanding of important habitat characteristics associated with population persistence, including specific wetland attributes.

The three main objectives of this thesis were:

- to conduct surveys for Gopher frogs and other pond-breeding amphibians to model species occupancy at ARWMA in relation to hydroperiod and canopy cover;
- (2) to estimate general annual trends in hydroperiods at ARWMA wetlands using current and historic satellite imagery and a measure of wetland inundation duration;
- (3) to develop a habitat suitability model, using habitat characteristics of known Gopher frog wetlands in Georgia and their terrestrial buffers, and then use this model to predict current Gopher frog habitat suitability among ARWMA wetlands.

History of the Focal Study Site

The Alapaha River Wildlife Management Area (ARWMA; Alapaha) is an approximately 2,800-hectare (ha) wildlife management area (WMA) in Irwin County, Georgia along the eastern bank of the Alapaha River (Figure 1.1). The property has been

known as both the Lentile Tract, in reference to a previous property owner, and the Snake Sanctuary, a study area which, in the 1970s, hosted extensive research on the Eastern indigo snake (*Drymarchon couperi*), a species granted federal protection in 1978 (U.S. Fish and Wildlife Service, 1978; Landers & Speake, 1980). ARWMA includes 1,912 ha of upland pine forest and 867 ha of bottomland hardwood forest, creek drains, and wetlands in the Atlantic Southern Loam Plains ecoregion of Georgia. This region is comprised of many areas with agriculturally important soils; low, flat, and poorly drained forests; and well-drained, sandy ridges with xeric vegetation communities (Griffith et al., 2001). The property was once managed as a pine plantation for turpentine production until the 1960s. According to historical accounts, the property would have been managed with fire periodically to achieve several objectives: to maintain a low understory that would prevent other trees and shrubs from competing with the longleaf, to improve access for turpentining, and to protect the trees from more damaging wildfires (Pyne, 1982; Earley, 2004). This management of the planted pine uplands likely would have included thinning and burning of longleaf and slash pine (Pinus elliotti), as well as the hardwoods, though no details of management history from that time are available to confirm.

By the 1960s and 1970s, following the decline of the turpentining industry in the South, southern forestry products company Rayonier converted the property for timber production. It was managed primarily as a slash pine plantation with some upland areas planted with sand pine. Slash pine remains the dominant forest type occurring on the property today. Rayonier reportedly burned the property on a 2–3-year rotation until the late 1980s (Matt Elliott, Georgia Department of Natural Resources, personal

communication). Historic aerial photographs from 1937, 1948, 1962, and 1972 provide some insight into the prior forestry practices that were conducted at Alapaha before the property was acquired by the state. In a 1937 aerial image, much of the property reflects the visual signature of cleared areas; remnant and, perhaps, thinned, longleaf pine forests; and shrub/scrub land cover (Figure 1.2). The most extensive clearing of land appears to have occurred between 1948 and 1962; windrows as well as orderly rows of newly planted pines can be interpreted from these images, and ditches now connect what previously appeared to be isolated wetlands. Several creek impoundments can be seen, and power lines now cross through the property in these 1962 images. By comparison, the forest cover provided by the planted pines that comprise the property today, as seen in 30-meter Landsat 8 satellite imagery collected from 2013 to the present or aerial imagery (Figure 1.3), greatly exceeds the forest cover that was present in the 1937-1972 imagery.

In the 1990s, Mr. Lentile worked with the Georgia Department of Natural Resources' Wildlife Resources Division to begin managing the property with the objective of restoring areas of longleaf pine, and, despite the dense matrix of planted pines and intensive agriculture that surrounds the property, ARWMA currently supports remnant populations of several priority wildlife species considered pine savanna ecosystem specialists, including the Gopher tortoise, Bachman's sparrow, Eastern indigo snake, Striped newt, and Gopher frog. In 2016, the property was purchased by the Georgia Department of Natural Resources, with assistance from several state, federal, and private partner organizations, in line with their initiative to expand and improve public lands for the protection of the Gopher tortoise, a declining keystone species (Georgia Department of Natural Resources, 2017). The property was established as the Alapaha

River Wildlife Management Area in the fall of 2016. Despite major land conversion of the area's former native longleaf pine ecosystem to plantation forestry, recent surveys have identified ARWMA as hosting the third largest population of Gopher tortoises in Georgia (Georgia Department of Natural Resources, 2017). With over 40 geographically isolated seasonal wetlands throughout the property and a report of a rare Gopher frog found on the property in 2013, there was hope that Alapaha may represent a stronghold, or at least an important conservation area, for Gopher frogs and other rare and declining pond-breeding amphibians, as well (Georgia Department of Natural Resources, unpublished data).

Literature Cited

- Brockway, D. G. (2005). *Restoration of longleaf pine ecosystems*: Asheville, NC: USDA Forest Service, Southern Research Station, 2005.
- Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. d., Rylands, A. B., Konstant, W. R., . . . Hilton-Taylor, C. (2002). Habitat Loss and Extinction in the Hotspots of Biodiversity. *Conservation Biology*(4), 909.
- Calhoun, D., McKee, A. M., Calhoun, D. L., Barichivich, W. J., Spear, S. F., Goldberg,
 C. S., & Glenn, T. C. (2015). Assessment of Environmental DNA for Detecting
 Presence of Imperiled Aquatic Amphibian Species in Isolated Wetlands. *Journal*of Fish and Wildlife Management, 6(2), 498-510.
- Chandler, H. C., Rypel, A. L., Jiao, Y., Haas, C. A., & Gorman, T. A. (2016).
 Hindcasting Historical Breeding Conditions for an Endangered Salamander in
 Ephemeral Wetlands of the Southeastern USA: Implications of Climate Change.
 PLoS ONE, 11(2), 1-17. doi:10.1371/journal.pone.0150169
- Cushman, S. A. (2006). Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation*, *128*(2), 231-240. doi:10.1016/j.biocon.2005.09.031
- Dodd, C. K. (1992). Biological diversity of a temporary pond herpetofauna in North Florida sandhills, *Biodiversity and Conservation* (1)125-142.
- Earley, L. S. (2004). *Looking for Longleaf: the fall and rise of an American forest*: Chapel Hill: University of North Carolina Press, ©2004.

- Erwin, K. J., Chandler, H. C., Palis, J. G., Gorman, T. A., & Haas, C. A. (2016).
 Herpetofaunal Communities in Ephemeral Wetlands Embedded within Longleaf
 Pine Flatwoods of the Gulf Coastal Plain. Southeastern Naturalist, 15(3), 431.
 doi:10.1656/058.015.0305
- Evans, J. P., Cecala, K. K., Scheffers, B. R., Oldfield, C. A., Hollingshead, N. A., Haskell, D. G., & McKenzie, B. A. (2017). Widespread Degradation of a Vernal Pool Network in the Southeastern United States: Challenges to Current and Future Management. *Wetlands*(6), 1093. doi:10.1007/s13157-017-0943-z
- Fahrig, L. (2001). How much habitat is enough? *Biological Conservation*, 100(1), 65-74.
- Fonseca, C. R., Coutinho, R. M., Azevedo, F., Berbert, J. M., Corso, G., & Kraenkel, R.
 A. (2013). Modeling Habitat Split: Landscape and Life History Traits Determine
 Amphibian Extinction Thresholds. *PLoS ONE*, 8(6), 1-7.
 doi:10.1371/journal.pone.0066806
- Franz, R. (1986). Gopherus polyphemus (Gopher tortoise) Burrow commensals.

 Herpetological Review, 17(3), 64-64.
- Frost, C. (2007). History and Future of the Longleaf Pine Ecosystem. In S. Jose, E. J. Jokela, & D. L. Miller (Eds.), *The Longleaf Pine Ecosystem*. New York, NY: Springer.
- Georgia Department of Natural Resources. (2017). *Alapaha River WMA: Storied site for sandhills*, *wildlife*. Retrieved from https://georgiawildlife.blog/2017/04/25/profile-alapaha-river-wma/
- Georgia Department of Natural Resources Wildlife Resources Division. (2015). *State Wildlife Action Plan*.

- Godley, J. S. (1992). Threatened: Gopher frog Rana capito LeConte. In P. E. Moler (Ed.), Rare and Endangered Biota of Florida (Vol. 3: Amphibians and Reptiles, pp. 15-19). Gainesville, FL: Univ. Press of Florida.
- Golden, H. E., Creed, I. F., Ali, G., Basu, N. B., Neff, B. P., Rains, M. C., . . .

 Christensen, J. R. (2017). Integrating geographically isolated wetlands into land management decisions. *Frontiers in Ecology and the Environment*, *15*(6), 319-327.
- Griffith, G. E., Omernik, J. M., Comstock, J. A., Lawrence, S., Martin, G., Goddard, A., .

 . . Foster, T. (2001). Ecoregions of Alabama and Georgia (Vol. (map scale
 1:1,700,000)). Reston, Virginia: U.S. Geological Survey.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., . . . Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*. 1(2), 1-9.
- Hammerson, G., & Jensen, J. B. (2004). Lithobates capito. *IUCN 2012. IUCN Red List of Threatened Species*. Retrieved from www.iucnredlist.org
- Hanski, I. (2005). *The Shrinking World: Ecological Consequences of Habitat Loss*Oldendorf/Luhe: International Ecology Institute.
- Hefner, J., & Brown, J. (1984). Wetland trends in the Southeastern United States.

 Wetlands, 4(1), 1-11.
- Jackson, D., & Milstrey, E. (1989). *The fauna of gopher tortoise burrows*. Paper presented at the Proceedings of the Gopher tortoise relocation symposium, Tallahassee (FL).

- Jensen, J. B., & Richter, S. C. (2005). Rana capito, Gopher Frog. In M. J. Lannoo (Ed.),

 Amphibian declines: the conservation status of United States species. Berkeley:

 University of California Press.
- Kramer, E., Conroy, M. J., Elliot, M. J., Anderson, E. A., Burnback, W. R., & Epstein., J. (2003). *The Georgia Gap Analysis Project Final Report*. Georgia Cooperative Fish and Wildlife Research Unit, Athens, GA.
- Landers, J. L., & Speake, D. W. (1980). Management Needs of Sandhill Reptiles in Southern Georgia. Proceedings of the Annual Conference, Southeastern Association of Fish and Wildlife Agencies (34) 515-29.
- Lane, C. R., & D'Amico, E. (2016). Identification of Putative Geographically Isolated

 Wetlands of the Conterminous United States. *Journal of the American Water*Resources Association(3), 705. doi:10.1111/1752-1688.12421
- Maerz, J. C., & Terrell, V. C. K. (2016) Status Assessment of Known Gopher Frog (Lithobates capito) Breeding Wetlands and Upland Habitats in Georgia. *A final report to the Georgia Department of Natural Resources*: University of Georgia.
- McCauley, L. A., Anteau, M. J., Post van der Burg, M., & Wiltermuth, M. T. (2015).

 Land use and wetland drainage affect water levels and dynamics of remaining wetlands. *Ecosphere*, 6(6).
- Newbold, T., Hudson, L. N., Hill, S. L., Contu, S., Lysenko, I., Senior, R. A., . . . Collen, B. (2015). Global effects of land use on local terrestrial biodiversity.

 *Nature(7545), 45.

- Noss, R. F., LaRoe, E. T., & Scott, J. M. (1995). Endangered ecosystems of the United States. [microform]: a preliminary assessment of loss and degradation:

 Washington, D.C.: U.S. Dept. of the Interior, National Biological Service, 1995.
- Outcalt, K. W. (2000). The Longleaf Pine Ecosystem of the South. *Native Plants Journal*(1), 42.
- Palis, J. G., & Fischer, R. A. (1997) Species Profile: Gopher Frog (*Rana capito* spp.) on Military Installations in the Southeastern United States. *Technical Report SERDP-97-5*.
- Peet, R. K., & Allard, D. J. (1993). Longleaf Pine Vegetation of the Southeastern Atlantic and Eastern Gulf Coast Regions: A Preliminary Classification. Paper presented at the Tall Timbers Fire Ecology Conference: the Longleaf Pine Ecosystem: ecology, restoration, and management, Tallahassee, FL.
- Peet, R. K., Platt, W. J., & Costanza, J. K. (2018). The ecology and management of fire-maintained savanna ecosystems of the Southeastern U.S. Coastal Plain. In W. Keeton & A. Barton (Eds.), *Ecology and Recovery of Eastern Old-Growth Forests*: Island Press.
- Perring, M. P., Standish, R. J., Price, J. N., Craig, M. D., Erickson, T. E., Ruthrof, K. X., Hobbs, R. J. (2015). Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere* 6(8):131
- Pyne, S. J. (1982). Fire in America: a cultural history of wildland and rural fire:

 Princeton, N.J.: Princeton University Press, ©1982.

- Quesnelle, P. E., Fahrig, L., & Lindsay, K. E. (2013). Effects of habitat loss, habitat configuration and matrix composition on declining wetland species. *Biological Conservation*, 160, 200-208. doi:10.1016/j.biocon.2013.01.020
- Redmond, W. H., & Scott, A. F. (1996). *Atlas of Amphibians in Tennessee*: Austin Peay State University.
- Richter, S. C., O Neill, E. M., Nunziata, S. O., Rumments, A., Gustin, E. S., Young, J. E., & Crother, B. I. (2014). Cryptic Diversity and Conservation of Gopher Frogs across the Southeastern United States. *Copeia*, 2(2), 231.
- Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer,
 G. (2002). The Human Footprint and the Last of the Wild. *BioScience*(10), 891.
 doi:10.1641/0006-3568(2002)052[0891:thfatl]2.0.co;2
- Semlitsch, R. D., Gibbons, J. W., & Tuberville, T. D. (1995). Timing of Reproduction and Metamorphosis in the Carolina Gopher Frog (*Rana capito capito*) in South Carolina. *Journal of Herpetology*, 29(4), 612-614. doi:10.2307/1564746
- Snodgrass, J. W., Komoroski, M. J., Jr, A. L. B., & Burger, J. (2000). Relationships among Isolated Wetland Size, Hydroperiod, and Amphibian Species Richness: Implications for Wetland Regulations. *Conservation Biology*, *14*(2), 414-419.
- Stuber, O. S., Kirkman, L. K., Hepinstall-Cymerman, J., & Martin, G. I. (2016). The ecological condition of geographically isolated wetlands in the southeastern United States: The relationship between landscape level assessments and macrophyte assemblages. *Ecological Indicators*, 62, 191-200.
- Tiner, R. W. (2003). Geographically isolated wetlands of the United States, *Wetlands* 23: 494-516.

- U.S. Fish and Wildlife Service. (1978). Endangered and threatened wildlife and plants:

 Listing of the Indigo Snake as a threatened species. Federal Register 43: 4026-4029.
- U.S. Fish and Wildlife Service. (1991). Status review of the gopher frog (Rana capito) InU.S. Fish and Wildlife Service Endangered Species Office (Ed.), (pp. 38 pp.).Jackson, Mississippi.
- USDA-NRCS. (2016). Longleaf Pine Initiative 2016 Progress Report.
- Van Lear, D. H., Carroll, W. D., Kapeluck, P. R., & Johnson, R. (2005). History and restoration of the longleaf pine-grassland ecosystem: Implications for species at risk, *Ecological Management*, 211: 150-165.
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human Domination of Earth's Ecosystems. *Science*, 277(5325), 494-499.
- Ware, S., Frost, C., & Doerr, P. (1993). Southern Mixed Hardwood Forest: The Former Longleaf Pine Forest. In A. C. Echternacht, S. G. Boyce, & W. H. Martin (Eds.), Biodiversity of the southeastern United States: Wiley.

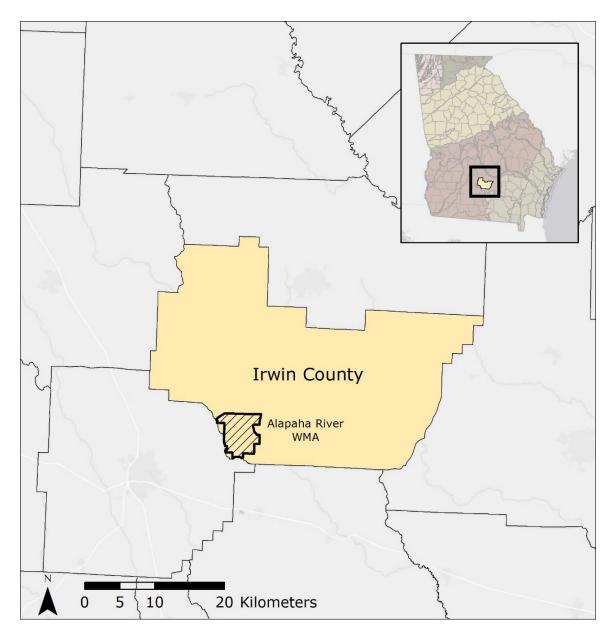


Figure 1.1: Study area of Alapaha River Wildlife Management Area in southwestern Irwin County, Georgia.



Figure 1.2: A composite of 1937 aerial photography overlaying present-day (Google Earth) imagery for southwestern Irwin County, with the Alapaha River providing the western and southern borders of what is now known as the Alapaha River Wildlife Management Area (boundary in orange). Aerial photographs from 1937, 1948, 1962, and 1972 were available for most of the spatial extent of the study area.



Figure 1.3: Present-day Google Earth imagery for southwestern Irwin County, with the heavily forested Alapaha River Wildlife Management Area bounded in orange.

CHAPTER 2

AMPHIBIAN OCCUPANCY AMONG WETLANDS WITHIN THE ALAPAHA RIVER WILDLIFE MANAGEMENT AREA

Introduction

Amphibian species of conservation concern are often distributed among remnant, highly fragmented landscapes, with species' known distributions limited to disjointed patches of habitat on lands where surveys have been conducted. A key first step for recovering species is to identify where they still occur and to study the environments which continue to support these extant populations. Understanding species-habitat relationships can help us discover new populations of rare or endangered species and can inform habitat management and restoration actions. Many pond-breeding species of amphibians exhibit complex life histories, requiring both terrestrial and aquatic habitats to complete different life stages, and their often cryptic behavior or morphology can make them difficult to detect in different habitats or at different life stages (Cott, 1940). Sampling designs for pond-breeding amphibians should incorporate species- and habitat-specific information to focus survey efforts to those habitats where species are most likely to occur and to use repeated methods that increase their detectability (Green, 2003; Barata, Griffiths, & Ridout, 2017).

Acoustic monitoring has become a standard technique used to monitor vocal anuran species (Heyer, 1994; Walls et al., 2004; Dorcas, Price, Walls, & Barichivich,

2010). Automated recording devices can be programmed to collect data from multiple sites simultaneously so that environmental conditions are contemporaneous across sites; in addition, automated recording devices collect data without the disturbance associated with manual call surveys (Steelman & Dorcas, 2010). Factors affecting calling behavior may differ between species, so call survey detection data and temporal or environmental covariates may be used to develop predictive models for identifying conditions wherein the target species is most likely to be detected (Steelman & Dorcas, 2010). Automated call surveys are a practical and efficient method for reliably detecting a species like the Gopher frog, *Rana capito*, which tends to call infrequently and within a short and unpredictable timeframe (Palis & Fischer, 1997; John B. Jensen, Bailey, Blankenship, & Camp, 2003). The Gopher frog's call is distinct—a long, low snore—and is easily distinguished from the calls of other species that comprise winter-breeding anuran assemblages throughout much of the Coastal Plain (Lannoo, Stiles, Saenz, & Hibbitts, 2018).

Like many rare and declining amphibians, Gopher frogs are relative habitat specialists. Gopher frogs typically breed within isolated, open-canopied wetlands with intermediate-to-long hydroperiods (J.B. Jensen & Richter, 2005). The geomorphology of these pond basins, paired with seasonal weather patterns for the southeastern U.S., historically resulted in these ponds filling with seasonal rains in fall and winter and drying sometime in the late spring or summer (Kirkman & Sharitz, 1994; Sutter & Kral, 1994). Seasonal drying limits the accumulation of predator and competitor communities (Pechmann, Scott, Whitfield Gibbons, & Semlitsch, 1989; Babbitt, 2005; Baldwin, Calhoun, & deMaynadier, 2006; Amburgey, Bailey, Murphy, Muths, & Funk, 2014) and

allows fire to pass through the basin to prevent tree and shrub encroachment (Cowardin, 1979; Ralph W. Tiner, 1993; Wellborn, Skelly, & Werner, 1996; Snodgrass, Komoroski, Jr, & Burger, 2000; R. W. Tiner, 2003; Skelly, Halverson, Freidenburg, & Urban, 2005; Baldwin et al., 2006; Thurgate & Pechmann, 2007). Today, without active management to maintain the open canopied structure of wetlands, many wetlands with shortened hydroperiods inevitably experience increased canopy cover (Thurgate & Pechmann, 2007; Lu, Sun, McNulty, & Comerford, 2009), which results in increased evapotranspiration that reduces the amount of water maintained within, thereby shortening the hydroperiod (Klaassen, 2001; Brooks, 2004). Tree and shrub canopies can also reduce the quality of detrital resources entering the wetland and reduce light that promotes algal production within the wetland (Skelly, Freidenburg, & Kiesecker, 2002; Skelly et al., 2005; Opsahl, Golladay, Smith, & Allums, 2010; Kuehn, Francoeur, Findlay, & Neely, 2014; Jones, McLaughlin, Henson, Haas, & Kaplan, 2018). Amphibian species exhibit different responses to canopy cover and hydroperiod, and a shift towards increased canopy closure and shortened wetland hydroperiods may be contributing to declines in some species and an overall loss in amphibian biodiversity (Pechmann et al., 1989; Raymond D. Semlitsch, Scott, Pechmann, & Gibbons, 1996; Thurgate & Pechmann, 2007; Liner, Smith, Golladay, Castleberry, & Gibbons, 2008; Enge & Farmer, 2014; Chandler, Rypel, Jiao, Haas, & Gorman, 2016).

The objectives of this study were to estimate current occupancy patterns of Gopher frogs and other pond-breeding amphibians among wetlands within the Alapaha River Wildlife Management Area (ARWMA) and to ascertain what factors currently determine amphibian occupancy among wetlands to inform future wetland and upland

management for priority species. ARWMA is an approximately 2,700-hectare (ha) tract in Irwin County, Georgia along the eastern bank of the Alapaha River (see detailed site description in Chapter 1). The property was once managed as a pine plantation for turpentine production until the 1960s and timber production through the 1980s. In the 1990s, management of portions of the property focused on restoring areas of longleaf pine. ARWMA currently supports remnant populations of several priority wildlife species considered pine savanna ecosystem specialists, including the Gopher tortoise, Bachman's sparrow, Eastern indigo snake, Striped newt, and Gopher frog. In 2016, the property was purchased by the Georgia Department of Natural Resources and established as the Alapaha River Wildlife Management Area. Aquatic habitats at Alapaha include cypress-gum ponds, herbaceous ponds, seasonal floodplain wetlands, wet flatwoods, bay swamps and creek swamps associated with the Alapaha River floodplain, and artificial impoundments and borrow pits (Figure 2.1). With more than 40 geographically isolated seasonal wetlands throughout the property and a report of a rare Gopher frog found on the property in 2013, there was hope that Alapaha may represent a stronghold, or at least an important conservation area, for Gopher frogs and other rare and declining pondbreeding amphibians.

Gopher frogs spend most of their lives underground in stump holes or subterranean burrows created by Gopher tortoises, small mammals, or crayfish, but they are most likely to be detected during breeding events when they make their way to wetland sites (Franz, 1986; J.B. Jensen & Richter, 2005). Gopher frog breeding activity has been documented in ephemeral to semipermanent ponds, including cypress ponds, emergent herbaceous wetlands, limesink ponds, sinkhole wetlands, sloughs, and borrow

pits, but the species is most frequently associated with seasonally inundated depression wetlands with shallow basins and emergent vegetation. Given sufficient rainfall, these basins, which may be dry for much of the year, are recharged in late fall or winter, providing pools of water free of the fish, amphibian, and invertebrate predators that typically occupy more permanent bodies of water (Pechmann et al., 1989; Raymond D. Semlitsch, Gibbons, & Tuberville, 1995; Saenz, Fitzgerald, Baum, & Conner, 2006; Adams et al., 2013). While Gopher frogs exhibit prolonged breeding in the southernmost part of their range (K. Enge, Florida Fish and Wildlife Conservation Commission, pers. comm.), throughout much of Alabama, Georgia, South Carolina, and North Carolina these frogs breed explosively in short bursts of breeding activity associated with rainfall during winter or early spring (John B. Jensen et al., 2003). The more explosive and seasonally restricted breeding activity observed across most of their range is likely related to their reliance on ephemerally inundated wetlands and the temporally limited availability of these habitats outside of peninsular Florida (K. Enge, Florida Fish and Wildlife Conservation Commission, and J. Jensen Georgia Department of Natural Resources, pers. comm.).

Methods

Selection and Characterization of Wetlands

Sampling sites included 24 ponds which were spatially distributed across the WMA and represented a gradient of both canopy cover and hydroperiod (Figure 2.2). Ponds sites were identified after reviewing the National Wetland Inventory, the National Hydrography Database, and the Georgia Department of Natural Resources wetland layer,

and preliminary site visits to select study ponds were conducted in September and October of 2016 when most seasonal wetlands were dry.

I selected 24 ponds or wetlands classified as cypress-gum ponds, herbaceous ponds, borrow pits, and shallow artificial impoundments (Hammerson & Jensen, 2004; J.B. Jensen & Richter, 2005). Pond canopy cover was estimated visually and categorized (<25%, <50%, >50%, >75%). I used site visits and analysis of historic and current aerial imagery, including 15- to 30-meter-resolution Landsat 7 and 8 satellite imagery collected between 1999 and 2017 and historic aerial photographs from 1937, 1948, 1962, and 1975, to determine whether ponds were hydrologically isolated and whether the hydrology of individual ponds was likely altered by any of several practices associated with agricultural and silvicultural land use, including ditching within and around ponds, the artificial creation of ponds (as in borrow pits or impoundments), or planting into the ecotone. In particular, I noted all stream connections and ditches within the pond basin or within 5 meters of ponds. For each pond, maximum water depth was recorded during each site visit between December 2016 through June 2017, and ponds were classified as "wet" when maximum water levels were greater than 5 cm and "dry" when less than 5 cm (Figure 2.3). A cut-off of 5 centimeters was selected for two logistical reasons: 1) dipnetting was inefficient, and 2) ponds with standing water less than 5 cm were usually dry within 48 hours in the absence of additional rainfall. For ponds which were never recorded as wet throughout the 2016-2017 sampling season, the hydroperiod was classified as dry; for ponds with ≥ 0 to <4 consecutive wet records, hydroperiods were classified as short; with >= 4 to < 8 consecutive wet records, hydroperiods were classified as intermediate; and with >= 8 wet records, hydroperiods were classified as long.

Amphibian Sampling

I used several methods to conduct amphibian surveys. I deployed automated recording devices, conducted encounter and egg mass surveys, and standardized dipnet sampling when water levels exceeded 5 cm. Sampling methods and time periods were designed to target Gopher frogs, while providing us with information about all pondbreeding amphibian species.

Acoustic monitoring with continuous sampling – Ponds were divided into two groups for acoustic monitoring, with each pond from one group paired with a nearby pond from the other group (between 88 m and 770 m apart), such that each of the two groups could independently represent the spatial distribution of ponds throughout ARWMA. With only 12 song meters available for use in this study, I could alternate their deployment between the two groups, while ensuring that I was collecting data from all areas of ARWMA with each night of sampling. Wildlife Acoustics Song Meters (models SM1 and SM4) were attached to trees at the edges of ponds ~1.5 m above the ground/water surface and facing the center of the pond. When sample ponds were located within 250 meters of another sample pond, the song meter was positioned on the opposite side of the pond to minimize the possibility of recording sounds from nearby ponds (Wildlife Acoustics, 2018). The song meters were programmed to collect a 5-min recording every 30 min from 1800 h to 2400 h and then every other hour from 2400 h until 0800 h every day. I chose five-minute recordings because this was consistent with the most commonly used manual anuran call survey protocols (Heyer, 1994; Dorcas et al., 2010). Song meters were first deployed in half the ponds on December 2016. Because I detected Gopher frogs at one pond during an early site visit, I left a song meter at that pond for the duration of the study. I rotated

12 other song meters between the half of the 23 other ponds every ~2-3 weeks. This sampling scheme allowed for the collection of data from a total of 24 ponds from December 2016 through June 2017. Site visits to collect and download data from the song meters and redeploy them at the alternate set of 12 ponds were conducted 8 times. I collected 20,538 samples totaling over 1,700 hours of recordings among the 24 ponds. Modeling Gopher frog detection for optimizing acoustic sample selection – In order to optimize efficient analysis of the 1,700 h of recordings, I modeled Gopher frog detection as a function of weather conditions at the one known occupied pond. I listened to all recordings from that pond between 1830 h and 2400 h for every day between 29 Dec 2016 and 3 April 2017 and analyzed spectrograms using Audacity Version 2.1.0 and Kaleidoscope Viewer Version 4.5.4 (open source software available at https://www.audacityteam.org/ and https://www.wildlifeacoustics.com/products/ kaleidoscope-software-acoustic). For each of the 5-min recordings collected during this period, I recorded Gopher frogs as detected (1) when I could hear or see their call and not detected (0) if I could neither hear nor see their call. I used this subset of the pond's detection and nondetection call data, along with temporal and environmental variables associated with each data point, to build a detection model that could be used to identify important predictor variables associated with Gopher frog calling patterns at Alapaha.

For building the detection model, I considered time of survey (time_t), julian date (julian_date), daily maximum and minimum temperature (maxtemp, mintemp), temperature at time of survey (temptime_t), daily precipitation (rainmm), number of days within a precipitation event (rain24hrs, rain48hrs, rain72hrs), and hours after sunset (hrsaftersunset). Daily precipitation data was extracted from the USGS streamgage

(USGS 02316000 Alapaha River), and minimum and maximum daily temperature data from the Bowen Research Farm at the Coastal Plain Experiment Station in neighboring Tift County. To generate hourly temperature values to estimate temperature at the time of survey for all recordings collected from the frogloggers, I used the following algorithm (Chow & Levermore, 2007):

$$T(t) = \left(\frac{T_{\text{MAX}} - T_{\text{MIN}}}{2}\right) \times \left[\cos\left(\frac{(t - t_{\text{max}})\pi}{t_{\text{max}} - t_{\text{min}}}\right) + 1\right] + T_{\text{MIN}}.$$
(7)

Where T_{MAX} and T_{MIN} = maximum and minimum daily temperature, and t_{max} and t_{min} = the time at which those temperatures are estimated to occur each day.

I used different combinations of ten different variables to develop a series of models that might explain Gopher frog calling patterns. I ran 11 different generalized linear models in R to identify the best predictors for when Gopher frogs were most likely to be detected when present (R Development Core Team, 2018; Table 2.1). I compared these models using Akaike Information Criterion (AIC), and the models which had a difference of <2 AIC relative to the model with the minimum AIC were considered to offer similar support (Burnham & Anderson, 2002).

Estimation of detection and occupancy for all anurans — Based on the results of the acoustic sample selection model, for each pond, I selected five, 5-min recordings collected on different days all within 48 hours of rain and when there was water in the pond or when the pond was likely to be wet. I first selected samples between 1630 h and 2400 h between 29 Dec 2016 and 3 April 2017. I excluded samples during heavy rainfall and high winds as these conditions limited the ability to detect anuran calling and are

known to negatively influence the probability of calling for many anuran species (Bridges & Dorcas, 2000; Saenz et al., 2006; Steelman & Dorcas, 2010). For a limited number of ponds with relatively few samples that fit the initial criteria, I selected recordings from later in the evening. I listened to these recordings and used visual analysis of spectrograms to assist with species identification when necessary, and I recorded all species heard calling during the sample.

I modeled detection and site occupancy for vocal anurans using the package 'unmarked' (Chandler & Fiske, 2011). Because sampling occasions were already selected using weather criteria to maximize Gopher frog detection, I did not include any weather covariates for detection in the occupancy analysis. I included two covariates, hydroperiod and canopy cover classifications, as ranked values (1-4) for each covariate (Table 2.2). Canopy cover values corresponded to the percentage of canopy cover within the pond: $1 = \langle 25\%, 2 = \langle 50\%, 3 = \langle 75\%, 4 = \rangle 75\%$. Hydroperiod was ranked similarly, with hydroperiod classifications determined by the number of days a basin was inundated. If a pond was never inundated throughout the study, it was classified as dry and ranked as 1. Other hydroperiod rankings were as follows: 2 = 30-90 days, 3 = 90-180 days, $4 = \rangle 180$ days.

Four models were developed for each species to explore the relative influence of hydroperiod and canopy cover for species occurrences. Model 1 was the null model; Model 2 stated that canopy cover classification influenced species occurrence; Model 3 stated that hydroperiod classification influenced species occurrence; and Model 4 stated that canopy cover and hydroperiod classification influenced species occurrence (Table 2.2). The December-to-April sampling timeframe likely captured a closed breeding

season for *Pseudacris crucifer*, *P. nigrita*, *P. ocularis*, *P. ornata*, *and R. capito*, and, potentially, a breeding pulse for *R. sphenocephala*, which can remain in wetlands year-round and breeding episodically fall through spring. I compared models using AICc (Burnham & Anderson, 2002). All analyses were performed using R (R Development Core Team, 2018).

Supplemental wetland sampling for amphibians – Standardized wetland surveys were used to detect amphibian species at all life stages and to monitor pond water levels (Figure 2.3). Surveys were conducted for each pond on eight sampling occasions, with site visits occurring every 3-to-4 weeks from December 2016 through June 2017. Species occurrence data, both for Gopher frogs and other pond-breeding amphibians, was collected during these visits via a variety of techniques, including dipnet surveys, egg mass surveys, and opportunistic auditory and visual encounters. Site visits and field surveys were conducted between the hours of 0800 and 0100. While much of the sampling was conducted during the day and in the absence of rain, efforts were made to ensure that all sites had the opportunity to be sampled at least once during rainy conditions and after sunset to increase detection of different species. When wet, ponds were surveyed with a dipnet (4 sweeps per acre with a minimum of 3 sweeps and a maximum of 30 sweeps for each pond). In addition, egg masses or adult amphibians observed visually or heard vocalizing were recorded. While regular trapping was not a standardized part of wetland surveys, minnow traps were deployed on several occasions, both at sites with longer hydroperiods and at sites with some hydrological connection to other waters. The presence and life stage of all amphibian species detected were

recorded. Recordings from song meters deployed in some of the longer-hydroperiod ponds after April 10 through June or until the ponds dried were also used to supplement inventories of those ponds.

Results

Characterization of ARWMA ponds

Of the 24 ponds sampled, 9 were classified as forested, 7 were classified as herbaceous, and 7 were classified as intermediate between forested and herbaceous (Table 2.3). Two ponds, one borrow pit and one impoundment, were classified as artificially-constructed. Canopy cover estimates for the different classifications of pond types ranged from 0% for artificial ponds; 0 to <25% for herbaceous; >50% to >75% for forested; and <50% to >75% for mixed forested/herbaceous. The National Wetland Inventory and the National Hydrography Database were the sources used to classify ponds as either forested or herbaceous, and these sources disagreed on the classification of 7 ponds, reclassified in this report as mixed forested/herbaceous. While the difference in classification between the two sources may relate to a difference in classification methodology, it is likely that the two different classifications for these 7 ponds represent differences in canopy cover over time, with earlier classifications assessing the more historic, herbaceous conditions prior to wetland succession. More than 60% (16 ponds) showed signs of hydrologic alteration (Table 2.3). The presence of fish was confirmed in two study ponds: 4 and 45. One site hosting predatory fish, pond 45, was a semipermanent-to-permanent borrow pit, and fish were detected on several sampling occasions. Pond 4 had a shallow basin and shorter observed hydroperiod, and fish were

detected on one sampling occasion, likely introduced via recent flooding from an adjacent creek swamp. Most areas around the ponds had been recently burned or were burned during the course of sampling, although most fires occurred when pond basins were inundated, so fire was largely excluded from the basins, particularly those with intermediate to long hydroperiods.

All but two of the sample ponds were dry prior to the start of this study. During the sampling period, 5 ponds were dry the entire period; 9 ponds held water for less than 90 days (short hydroperiod); 7 ponds held water for 90 to 180 days (intermediate hydroperiod), and 3 ponds held water for the entire study period (semi-permanent or long hydroperiods), Based on additional site visits, these three ponds held water for at least nine months or longer (Figure 2.3).

Acoustic detection of Gopher frogs

On January 25 during a site visit, I detected a Gopher frog calling at pond 3. I listened to and analyzed the 236 audio recordings totaling 1,180 minutes between 25 January 2017 through 17 February 2017. I was able to detect a Gopher frog calling in 93 recordings, with the last detections occurring on 13 February 2017. Importantly, no overlapping calls were recorded at any given time. Assuming that Gopher frogs occupied this pond for all 20 d between the first and last detection, the top models for Gopher frog detection were Model 4 which included rain within 48 h + temperature + hours past sunset (AICc = 277.24) and Model 3 which included rain within 48 h + temperature (AICc = 277.91) (Table 2.4). Gopher frog detection decreased with increasing temperature, likely reflecting lower detection later in the breeding window, and increased substantially within 48 of rain (Figure 2.4). Mean probability of detection was 0.69 for 5-min

recordings collected within 48 h of rain, but only 0.24 when there was no rain within the prior 48 hours. Therefore, using five 5-min recordings collected within 48 h of rain during this 20-d window, the probability of detecting a Gopher frog calling at least once was 0.997 (Figure 2.5).

Winter breeding anuran occupancy based on acoustic sampling

In total, I processed 2,965 minutes of audio files (593 five-minute recordings) collected between the dates of 29 December 2016 and 3 April 2017 from the 24 study ponds. All six species for which occupancy and detection were modeled were detected calling between December and April among the 24 ponds (Table 2.4). Gopher frogs were only detected at a single pond, pond 3.

The estimated probability of detection for Gopher frogs (*R. capito*) was 0.355 (se = 0.748) and estimated occupancy for *R. capito* at ARWMA was only 0.046, and (Figure 2.6). Because *R. capito* were detected at only one site, the null model (Model 1) was the best fitting model for estimating occupancy for *R. capito* (Table 2.6). Overall occupancy for *P. nigrita* was the second lowest, 0.301 with 0.497 detection, and the null model was again the best fit (Table 2.4, Figure 2.6). *Pseudacris crucifer* had the highest probability of detection (0.746) and occupancy (0.792). Probabilities of detection for *R. sphenocephala*, *P. ornata*, *P. ocularis* were 0.53, 0.345, and 0.468, respectively, and occupancy for *R. sphenocephala*, *P. ornate*, and *P. ocularis* was similarly high at 0.767, 0.763, and 0.734, respectively. The top model for *P. crucifer* occupancy included canopy cover and hydroperiod rank (Model 4), though canopy cover had a nominal effect while hydroperiod rank had a strong positive effect on occupancy. For *R. sphenocephala*, *P. ornata*, and *P. ocularis*, top occupancy models all included only hydroperiod rank, Model

3 (Figure 2.7). As with *P. crucifer*, occupancy of all three species increased with increasing hydroperiod rank (e.g., *R. sphenocephala* Figure 2.6).

Supplementary amphibian surveys

In total, 16 species of anurans and 6 species of caudates were detected via surveys or opportunistic encounters among the 24 study ponds (Table 2.3, Figure 2.8). *Hyla chrysoscelis* was not detected at a study pond, but it was detected calling within an area of mixed hardwood forests during a site visit while en route to a study pond. The most frequently detected species within study ponds were *P. ocularis*, which was regularly detected calling even from dry pond basins, and *P. ornata* adults, which were detected within most study ponds (Table 2.3). *P. ornata* tadpoles were detected in only ponds 1 and 3. Both species were detected at 21 out of the 24 sites sampled; they were not found at ponds 14, 36, or 43. The third most frequently detected species was *R. sphenocephala*, which was detected at all 19 ponds which were recorded as wet on one or more sampling occasions.

Gopher frogs were detected at a single site, pond 3, primarily via recorded call surveys; however, Gopher frogs were detected by other methods on three occasions. A Gopher frog was heard during a site visit to pond 3 on 25 January 2017 and 26 January 2017. A single Gopher frog was visually detected on 20 January around 1900 h traveling under moderately rainy conditions along the edge of a cypress wetland alongside a dirt road on the north side of a powerline easement between pond 3 and pond 4 (Figure 2.11).

Other species that were encountered infrequently and at the fewest sites were *Notophthalmus perstriatus, Scaphiopus holbrookii, and Ambystoma tigrinum.* On 11 March 2017, a single adult *N. perstriatus* was captured in a dipnet in pond 18. *S.*

holbrookii tadpoles were detected in pond 46 in late-summer 2017 (Figure 2.12). *A. tigrinum* eggs and larvae were detected in ponds 3, 4, 30, and 31.

Discussion

While a single year of field surveys cannot be conclusive, it seems apparent that Gopher frogs are currently restricted to a single breeding pond, pond 3, at ARWMA, and the current population size at pond 3 is likely small. This study was conducted following an extended drought, and winter rains did not sufficiently fill the basins of many ponds surveyed (US Drought Monitor, National Drought Mitigation Center, United State Department of Agriculture and National Oceanographic and Atmospheric Association 2018; Figure 2.9). Gopher frogs may skip years when environmental conditions are unfavorable, but Gopher frog calling was detected at one ARWMA pond, pond 3, and Gopher frogs bred at other sites in Georgia in the winter and spring of 2017 (J. Jensen, Georgia Department of Natural Resources, pers. comm.). Despite frequent focal visits to ponds and extensive acoustic sampling, I never detected multiple overlapping calling Gopher frog males, and I had only one visual sighting. Further, despite extensive Gopher tortoise burrow surveys by GDNR on ARWMA during my study period, no Gopher frogs were detected in upland burrow habitats. Therefore, the occupancy of Gopher frogs appears to reflect low abundance on the site rather than a result of low detectability. Our model showed high detectability for Gopher frog males during optimal conditions, and estimated occupancy for other species among the same wetlands was high for other syntopic species; between 0.70 and 0.80 for *P. crucifer*, *P. ocularis*, *P. ornata*, and *R.* sphenocephala.

The low occupancy and apparent low abundance of Gopher frogs at ARWMA is likely a product of the short hydroperiod at many wetlands. By April most of the ponds were dry, and I had notably fewer detections of spring and summer breeding amphibian species. Though I was unable to model the effects of hydroperiod on Gopher frog occupancy because they occurred at a single pond, occupancy of four of the other six species I modeled at ARWMA was clearly linked to increasing pond hydroperiod. Therefore, the observed short hydroperiods at most ponds and the relationship between hydroperiod and other concurrent breeding species suggest that hydroperiod is currently an important factor affecting Gopher frog and other anuran occupancy at ARWMA.

There are additional attributes about the one pond, pond 3, where Gopher fogs were detected that are connected to their current distribution on ARWMA. Pond 3 has a portion of the pond that remains open and densely herbaceous (significant cover of maidencane, *Panicum hemitomon*), which is typical of Gopher frog breeding ponds at other sites within Georgia (Figure 2.11). Serendipitously, this open portion of this single pond exists due to the maintenance of a power line across the northern portion of ARWMA. Were it not for this power line opening, it is likely that pond 3 would be a fully forested cypress-gum pond and unsuitable for Gopher frogs, and the population might have been extirpated from the site. Without immediate actions, the probability of persistence of Gopher frogs at ARWMA is likely low. Improving the probability of persistence of ARWMA's Gopher frog population will likely require wetland restoration, notably restoring the hydroperiod of many wetlands through repairing historic physical alterations and reducing the tree cover within the pond basins and the surrounding uplands. Given the apparent low abundance of frogs, habitat restoration will likely

require complementary population supplementation and facilitated dispersal (translocations) among restored wetlands.

The historic conversion of grasslands to dense pine forests managed for timber production carries forth numerous impacts to wetlands, including soil disturbance, groundwater withdrawals, water pollution and sedimentation, and changes in wetlands' hydrologic connectivity, vegetative structure, and hydropattern (R. W. Tiner, 2003; Skelly et al., 2005; Lu et al., 2009; Johnson, Barrett, Homyack, & Baldwin, 2016). These historic and ongoing land use practices influence the quality and availability of wetland habitats at ARWMA, and, of particular note in this study, the hydrology of wetland habitats. I have concluded from my research that a majority of ponds at ARWMA likely do not receive or hold as much water for as long as they would have historically. Gopher frogs require a minimum of ~100 days for larval development, though longer periods may be needed depending on wetland productivity and competitor densities. Other priority amphibian species such as striped newts require longer periods for larval development, and their populations may be dependent on periodic, multi-year hydroperiods that support paedomorphic life stages prior to metamorphosis. Recent studies concerned with conservation of pond-breeding amphibians in the U.S. identify the need to preserve longer-hydroperiod wetlands as they are more likely to support source populations that can buffer regional population dynamics, particularly in years of drought (Baldwin et al., 2006; H. C. Chandler et al., 2016). At ARWMA, high forest cover within ponds and the surrounding uplands likely contribute to shorter hydroperiods. In addition, historic ditching causes several large ponds on the property to drain (ponds 10 and 8), limiting the capacities of those ponds to hold water for extended periods (Figure 2.3,

Figure 2.10). Restoring the morphology of those ponds by eliminating the ditches, removing hardwoods and pines from pond basins, and reducing tree densities in the uplands should extend the hydroperiod of many wetlands, making them more suitable for Gopher frogs and other amphibian species (R. D. Semlitsch, 2000; Klaassen, 2001; Bryant, Bhat, & Jacobs, 2005; Freeman & Jose, 2009; Lu et al., 2009; Jones et al., 2018).

Literature Cited

- Adams, M. J., Miller, D. A. W., Muths, E., Corn, P. S., Grant, E. H. C., Bailey, L. L., . . . Walls, S. C. (2013). Trends in Amphibian Occupancy in the United States. *PLoS ONE*, 8(5), 1-5. doi:10.1371/journal.pone.0064347
- Amburgey, S. M., Bailey, L. L., Murphy, M., Muths, E., & Funk, W. C. (2014). The effects of hydropattern and predator communities on amphibian occupancy. *Canadian Journal of Zoology*, 92(11), 927-937. doi:10.1139/cjz-2014-0106
- Babbitt, K. J. (2005). The relative importance of wetland size and hydroperiod for amphibians in southern New Hampshire, USA. *Wetlands Ecology and Management*, 13(3), 269.
- Baldwin, R. F., Calhoun, A. J. K., & deMaynadier, P. G. (2006). The significance of hydroperiod and stand maturity for pool-breeding amphibians in forested landscapes. *Canadian Journal of Zoology*(11), 1604.
- Barata, I. M., Griffiths, R. A., & Ridout, M. S. (2017). The power of monitoring: optimizing survey designs to detect occupancy changes in a rare amphibian population. *Scientific Reports* 7 (1), 16491
- Bridges, A. S., & Dorcas, M. E. (2000). Temporal Variation in Anuran Calling Behavior: Implications for Surveys and Monitoring Programs. *Copeia*(2), 587-592.
- Brooks, R. T. (2004). Weather-related effects on woodland vernal pool hydrology and hydroperiod, *Wetlands*(24), 104-114

- Bryant, M. L., Bhat, S., & Jacobs, J. M. (2005). Measurements and modeling of throughfall variability for five forest communities in the Southeastern US. *Journal of Hydrology*, 312(1-4), 95-108. doi:10.1016/j.jhydrol.2005.02.012
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. 2nd Edition, New York: Springer-Verlag.
- Chandler, H. C., Rypel, A. L., Jiao, Y., Haas, C. A., & Gorman, T. A. (2016).
 Hindcasting Historical Breeding Conditions for an Endangered Salamander in
 Ephemeral Wetlands of the Southeastern USA: Implications of Climate Change.
 PLoS ONE, 11(2), 1-17. doi:10.1371/journal.pone.0150169
- Chandler, R., & Fiske, I. (2011). unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, 43(10), 1-23.
- Chow, D. H. C., & Levermore, G. J. (2007). New algorithm for generating hourly temperature values using daily maximum, minimum and average values from climate models. *Building Services Engineering Research and Technology*, 28(3), 237.
- Cott, H. B. (1940). *Adaptive coloration in animals*: London, Methuen & Co., London, UK.
- Cowardin, L. M. (1979). Classification of wetlands and deepwater habitats of the United States: Washington, D.C.: Fish and Wildlife Service, U.S. Dept. of the Interior.

- Dorcas, M. E., Price, S. J., Walls, S. C., & Barichivich, W. J. (2010). Auditory monitoring of anuran populations. In J. C. Kenneth Dodd (Ed.), *Amphibian ecology and conservation: a handbook of techniques*. New York: Oxford.
- Enge, K. M., A. L. Farmer, J. D. Mays, T. D. Castellón, E. P. Hill, and P. E. Moler..
 (2014). Survey of winter-breeding amphibian species. Final report, Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute,
 Lovett E. Williams, Jr. Wildlife Research Laboratory, Gainesville, Florida, USA.
 136pp.
- Franz, R. (1986). *Gopherus polyphemus* (Gopher tortoise) Burrow commensals. *Herpetological Review*, 17(3), 64-64.
- Freeman, J. E., & Jose, S. (2009). The role of herbicide in savanna restoration: Effects of shrub reduction treatments on the understory and overstory of a longleaf pine flatwoods. *Forest Ecology and Management*, 257, 978-986.

 doi:10.1016/j.foreco.2008.10.041
- Green, D. M. (2003). The ecology of extinction: population fluctuation and decline in amphibians. *Biological Conservation*, 111(3), 331.
- Hammerson, G., & Jensen, J. B. (2004). Lithobates capito. *IUCN 2012. IUCN Red List of Threatened Species*. Retrieved from www.iucnredlist.org
- Heyer, W. R. (1994). *Measuring and monitoring biological diversity*. Washington: Smithsonian Institution Press.
- Jensen, J. B., Bailey, M. A., Blankenship, E. L., & Camp, C. D. (2003). The Relationship between Breeding by the Gopher Frog, Rana capito (Amphibia: Ranidae) and Rainfall. *The American Midland Naturalist*, *150*(1), 185.

- Jensen, J. B., & Richter, S. C. (2005). Rana capito, Gopher Frog. In M. J. Lannoo (Ed.),

 Amphibian declines: the conservation status of United States species. Berkeley:

 University of California Press.
- Johnson, B. A., Barrett, K., Homyack, J. A., & Baldwin, R. F. (2016). Anuran occupancy and breeding site use of aquatic systems in a managed pine landscape. *Forest Ecology and Management*, *368*, 45-54. doi:10.1016/j.foreco.2016.03.004
- Jones, C. N., McLaughlin, D. L., Henson, K., Haas, C. A., & Kaplan, D. A. (2018). From salamanders to greenhouse gases: does upland management affect wetland functions? *Frontiers in Ecology and the Environment*, 16(1), 14-19.
- Kirkman, L. K., & Sharitz, R. R. (1994). Vegetation Disturbance and Maintenance of Diversity in Intermittently Flooded Carolina Bays in South Carolina. *Ecological Applications*(1), 177. doi:10.2307/1942127
- Klaassen, W. (2001). Evaporation from rain-wetted forest in relation to canopy wetness, canopy cover, and net radiation. *Water Resources Research*, *37*(12), 3227-3236. doi:10.1029/2001WR000480
- Kuehn, K. A., Francoeur, S. N., Findlay, R. H., & Neely, R. K. (2014). Priming in the microbial landscape: periphytic algal stimulation of litter-associated microbial decomposers. *Ecology*, *95*(3), 749-762.
- Lannoo, M. J., Stiles, R. M., Saenz, D., & Hibbitts, a. T. J. (2018). Comparative Call Characteristics in the Anuran Subgenus Nenirana. *Copeia*, 106(4).
- Liner, A. E., Smith, L. L., Golladay, S. W., Castleberry, S. B., & Gibbons, J. W. (2008).

 Amphibian Distributions within Three Types of Isolated Wetlands in Southwest

- Georgia. *American Midland Naturalist*, 160(1), 69-81. doi:10.1674/0003-0031(2008)160[69:ADWTTO]2.0.CO;2
- Lu, J., Sun, G., McNulty, S. G., & Comerford, N. B. (2009). Sensitivity of pine flatwoods hydrology to climate change and forest management in Florida, USA. *Wetlands*, 29(3), 826–836
- Opsahl, S. P., Golladay, S. W., Smith, L. L., & Allums, S. E. (2010). Resource-Consumer Relationships and Baseline Stable Isotopic Signatures of Food Webs in Isolated Wetlands, *Wetlands*, *30*: 1213–1224.
- Palis, J. G., & Fischer, R. A. (1997). Species profile [microform]: Gopher frog (Rana capito spp.) on military installations in the southeastern United States / by John
 G. Palis, Richard A. Fischer: Vicksburg, Miss.: US Army Corps of Engineers,
 Waterways Experiment Station; [Springfield, VA: Available from National Technical Information Service, 1997].
- Pechmann, J., Scott, D., Whitfield Gibbons, J., & Semlitsch, R. (1989). Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. *Wetlands Ecology & Management, 1*(1), 3.
- R Development Core Team. (2018). Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org
- Saenz, D., Fitzgerald, L. A., Baum, K. A., & Conner, R. N. (2006). Abiotic Correlates of Anuran Calling Phenology: The Importance of Rain, Temperature, and Season.

 Herpetological Monographs, 64.
- Semlitsch, R. D. (2000). Principles for management of aquatic breeding amphibians. *Journal of Wildlife Management*, 64, 615-631.

- Semlitsch, R. D., Gibbons, J. W., & Tuberville, T. D. (1995). Timing of Reproduction and Metamorphosis in the Carolina Gopher Frog (Rana capito capito) in South Carolina. *Journal of Herpetology*, 29(4), 612-614. doi:10.2307/1564746
- Semlitsch, R. D., Scott, D. E., Pechmann, J. H. K., & Gibbons, J. W. (1996). Structure and dynamics of an amphibian community. In M.L. Cody & J.A. Smallwood (Eds.), *Long-Term Studies of Vertebrate Communities* (pp. 217-248). San Diego, California: Academic Press.
- Skelly, D. K., Freidenburg, L. K., & Kiesecker, J. M. (2002). Forest canopy and the performance of larval amphibians. *Ecology*, 83(4), 983.
- Skelly, D. K., Halverson, M. A., Freidenburg, L. K., & Urban, M. C. (2005). Canopy closure and amphibian diversity in forested wetlands. *Wetlands Ecology and Management*, 13(3), 261-269.
- Snodgrass, J. W., Komoroski, M. J., Jr, A. L. B., & Burger, J. (2000). Relationships among Isolated Wetland Size, Hydroperiod, and Amphibian Species Richness:
 Implications for Wetland Regulations. *Conservation Biology*, 14(2), 414-419.
- Steelman, C. K., & Dorcas, M. E. (2010). Anuran Calling Survey Optimization:

 Developing and Testing Predictive Models of Anuran Calling Activity. *Journal of Herpetology*(1), 61.
- Sutter, R. D., & Kral, R. (1994). The ecology, status, and conservation of two non-alluvial wetland communities in the south Atlantic and eastern Gulf coastal plain, USA. *Biological Conservation*, 68, 235-243.

- Thurgate, N. Y., & Pechmann, J. H. K. (2007). Canopy Closure, Competition, and the Endangered Dusky Gopher Frog. *Journal of Wildlife Management*, 71(6), 1845-1852. doi:10.2193/2005-586
- Tiner, R. W. (1993). Using Plants as Indicators of Wetland. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 240.
- Tiner, R. W. (2003). Geographically isolated wetlands of the United States. *Wetlands* 23: 494-516.
- Walls, S. C., Hardin Waddle, J., Barichivich, W. J., Bartoszek, I. A., Brown, M. E., Hefner, J. M., & Schuman, M. J. (2004). Anuran site occupancy and species richness as tools for evaluating restoration of a hydrologically-modified landscape. *Journal of Agricultural, Biological, and Environmental Statistics*(3), 300.
- Wellborn, G. A., Skelly, D. K., & Werner, E. E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecological Systems*, 27, 337-363.
- Wildlife Acoustics. (2018). Song Meter SM4 Bioacoustics Recorder User Guide.

 Retrieved from Maynard, MA:

Table 2.1: Environmental variables included in candidate models for developing Gopher frog detection model: temperature at time of survey (temptime_t), daily precipitation (rainmm), number of days within a precipitation event (rain24hrs, rain48hrs), and hours after sunset (hrsaftersunset).

Model	temp at time of survey	daily precipitation	24 hours within rain	48 hours within rain	# hours after sunset
null					
1	×	×	×		
2	×		×		
3	×			×	
4	×			×	×
5		×	×		
6				×	×
7					×
8		×			×
9	×		×		×
10			×		

Table 2.2: Models developed to explore the relative influence of hydroperiod and canopy cover for species occurrences of six vocal anurans.

Model	Hypothesis
1	Null
2	Occupancy is a function of canopy cover
3	Occupancy is a function of hydroperiod
4	Occupancy is a function of canopy cover and hydroperiod

Table 2.3: Study pond characteristics and amphibian species inventories.

Pond ID	Area (ha)	Pond type ¹	Canopy rank ²	Hydro rank ³	Hydro Altered	Acris gryllus	Anaxyrus quercicus	Anaxyrus terrestris	Gastrophryne carolinensis	Hyla cinerea	Hyla femoralis	Hyla gratiosa	Hyla squirella	Pseudacris crucifer	Pseudacris nigrita	Pseudacris ocularis	Pseudacris ornata	Rana capito	Rana catesbeiana	Rana clamitans	Rana sphenocephala	Scaphiopus holbrookii	Ambystoma talpoideum	Ambystoma tigrinum	Eurycea quadridigitata	Notophthalmus perstriatus	Notophthalmus viridescens	Siren intermedia
1	0.61	Н	1	3	yes	×					×		×	×	×	×	×				×							
2	1.02	Н	1	3	yes	×					×		×	×	×	×	×			×	×							
3	1.36	Н	1	3	yes	×					×			×	×	×	×	×		×	×		×	×	×			
4	0.34	Н	1	3*	yes						×			×	×	×	×		×		×		×	×				
8	2.24	F	3	2	yes		×							×		×	×				×							
10	4.82	F	3	2	yes	×								×	×	×	×				×							
14	1.19	Н	1	1	no																							
15	1.29	F	4	2	no	×								×		×	×				×							
18	2.15	F	4	3	yes	×		×			×			×	×	×	×				×					×	×	
20	1.24	F	3	2	yes									×	×	×	×				×							
23	1.22	F	4	2	yes	×								×		×	×				×							
24	0.65	M	2	4	no	×	×		×		×	×	×	×	×	×	×		×		×				×			×
25	0.52	Н	1	2	no	×								×	×	×	×		×		×							
29	0.78	M	3	2	no											×	×				×							
30	1.73	M	3	3	yes	×								×	×	×	×				×			×			×	×
31	2.90	M	3	2	yes									×	X	×	X				×			×	×			
35	1.35	M	4	1	no						×		×	×		×	×					-						
36	1.33	H	1	1	yes																							
41	0.73	F	4	2	no									×		×	X				×							
42	1.81	F	4	3	yes						×			X		×	X				X							
43	4.67	M	2	1	yes																							
44	1.07	F	4	1	no											×	X											
45	0.38	Α	1	4*	yes	×		×		X			×	×	X	×	X		×		×							
46	1.41	A	1	4	yes	×	X			X	×	X	X	X	X	×	X		×	X	X	X			×			×

 $^{^1}$ pond type: H=herbaceous pond, F=forested pond, M=mixed herbaceous-forested, A=artificial 2 canopy cover rank: 1 = <25%, 2 = <50%, 3 = <75%, 4 = >75% 3 hydroperiod rank: 1 = dry, 2 = 30-90 days, 3 = 90-180 days, 4 = >180 days *fish detected

Table 2.4: Model selection results for the Gopher frog detection model including the number of parameters (K), Akaike's Information Criterion for small sample sizes (AICc), Δ AICc, model weight (w), and cumulative model weight. Models were ranked by AICc (Burnham & Anderson, 2002).

Model	K	AICc	ΔAICc	w	Cumulative w
4	4	277.24	0.00	0.54	0.54
3	3	277.91	0.67	0.39	0.94
6	3	281.77	4.53	0.05	1.00
9	4	297.37	20.12	0.00	1.00
2	3	298.89	21.64	0.00	1.00
1	4	300.36	23.12	0.00	1.00
10	2	302.95	25.71	0.00	1.00
5	3	304.42	27.18	0.00	1.00
8	3	311.12	33.88	0.00	1.00
11	1	318.50	41.26	0.00	1.00
7	2	318.66	41.41	0.00	1.00

Table 2.5: Model selection results for occupancy models for six species of winter-breeding vocal anurans including the number of parameters (K), Akaike's Information Criterion for small sample sizes (AICc), Δ AICc, model weight (w), and cumulative model weight.

Species	Model	K	AICc	ΔAICc	W	Cumulative
						w
Pseudacris crucifer	3	3	124.70	0.00	0.59042	0.59
	4	4	125.45	0.75	0.40650	1.00
	1	2	135.91	11.21	0.00217	1.00
	2	3	137.65	12.94	0.00091	1.00
Pseudacris nigrita	3	3	79.85	0.00	0.36	0.36
	2	3	80.71	0.87	0.23	0.59
	4	4	80.83	0.98	0.22	0.80
	1	2	81.05	1.20	0.20	1.00
Pseudacris ocularis	3	3	144.61	0.00	0.650	0.65
	4	4	146.31	1.70	0.278	0.93
	1	2	149.69	5.08	0.051	0.98
	2	3	151.50	6.89	0.021	1.00
Pseudacris ornata	3	3	125.42	0.00	0.72781	0.73
	4	4	127.40	1.98	0.27021	1.00
	1	2	137.88	12.46	0.00143	1.00
	2	3	139.83	14.41	0.00054	1.00
Rana capito	2	3	18.82	0.000	0.35	0.35
	1	2	18.85	0.034	0.35	0.70
	3	3	20.32	1.509	0.17	0.86
	4	4	20.70	1.880	0.14	1.0
Rana	4	4	135.81	0.00	5.2e-01	0.52
sphenocephala	3	3	136.01	0.20	4.8e-01	1.00
-	1	2	154.29	18.47	5.1e-05	1.00
	2	3	156.06	20.25	2.1e-05	1.00

Table 2.6: Occupancy (psi) and detection probabilities estimated for six species of vocal anurans across Alapaha River WMA.

Species	Model	psi	Lower 95% CI	Upper 95% CI	(p)	SE
Pseudacris crucifer	3	0.792	0.586	0.911	0.746	0.558
Pseudacris nigrita	1	0.301	0.149	0.513	0.497	0.590
Pseudacris ocularis	3	0.734	0.509	0.880	0.468	0.560
Pseudacris ornata	3	0.763	0.462	0.923	0.345	0.560
Rana capito	1	0.046	0.006	0.281	0.355	0.748
Rana sphenocephala	4	0.767	0.548	0.911	0.543	0.553

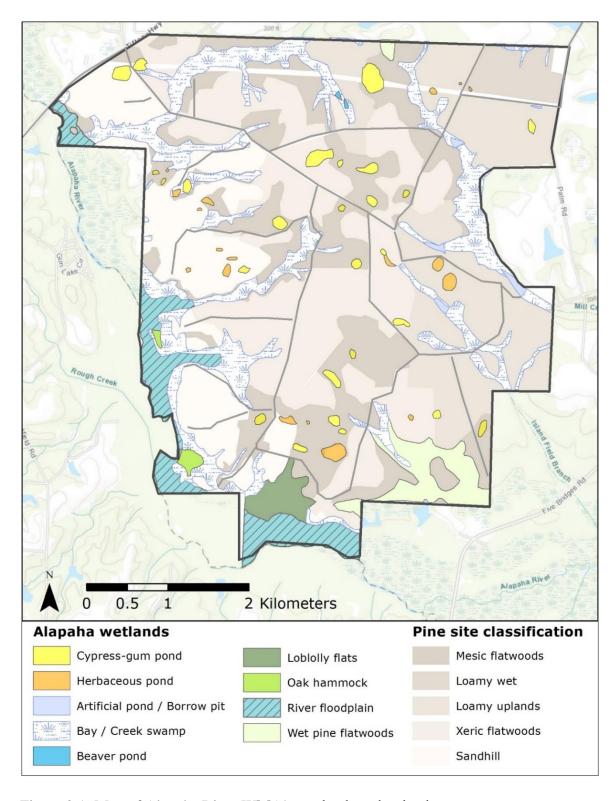


Figure 2.1: Map of Alapaha River WMA's wetlands and uplands.

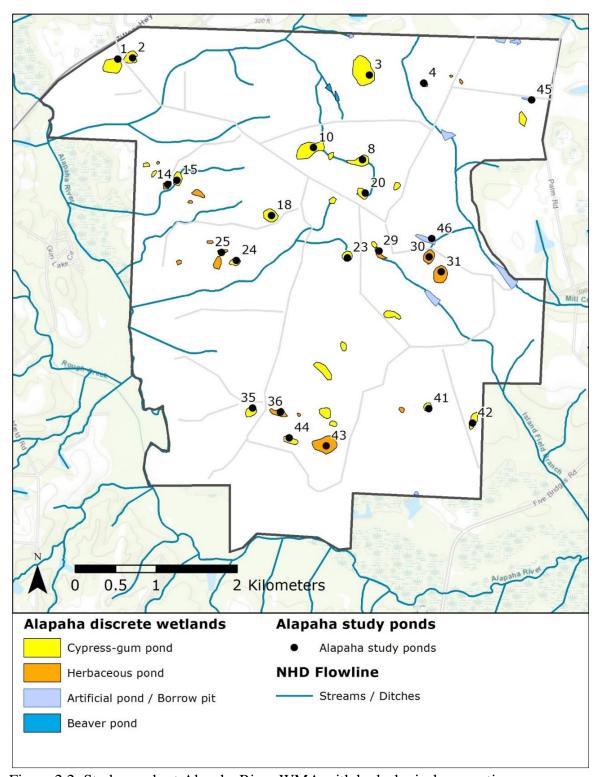


Figure 2.2: Study ponds at Alapaha River WMA with hydrological connections highlighted.

Pond #	Survey 1	Survey 2	Survey 3	Survey 4	Survey 5	Survey 6	Survey 7	Survey 8		
#	26-28	19-21	11-13	9-11	2-4	22-24	18-20	18-20		
	Dec	Jan	Feb	Mar	Apr	Apr	May	Jun		
	2016	2017	2017	2017	2017	2017	2017	2017		
45										
24										
46										
2										
1										
4										
3										
30										
42										
18										
31										
15										
8										
10										
25										
41										
20										
23										
29										
14										
36										
44										
43										
35										
we						wet (surface water detected)				
dry (no surface water detected)										

Figure 2.3: Record of surface water presence for study ponds in 2016-2017. If the maximum depth of surface water exceeded 5 centimeters, the pond was recorded as wet for that visit. Pond hydroperiod data are represented in order of longest-to-shortest recorded hydroperiods. The last five ponds included in the table were never inundated over the period of study and were recorded as dry upon each visit.

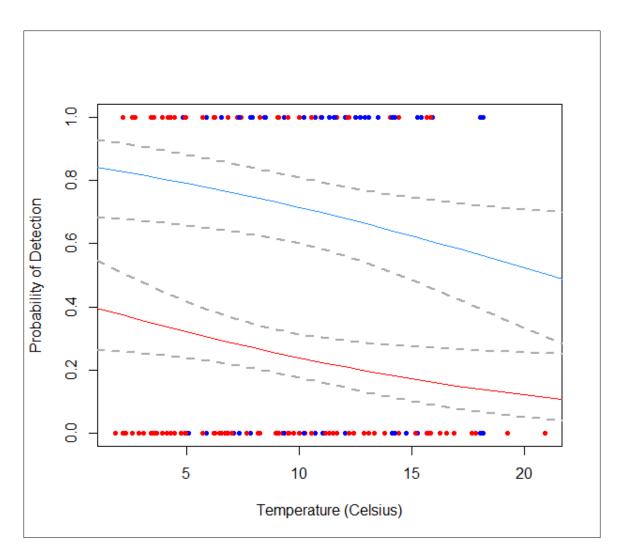


Figure 2.4: Probability of detecting Gopher frogs with rain within 48 hours (blue) and without rain within 48 hours (red), where temperature (temptime_t) is the continuous variable.

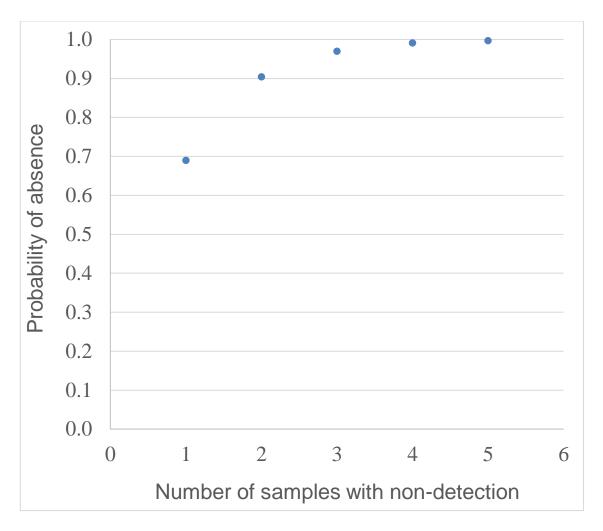


Figure 2.5: Mean probability that Gopher frogs are absent from a pond given a consecutive number of non-detections among five independent, 5-minute acoustic surveys collected after dark and within 48 h of rain.

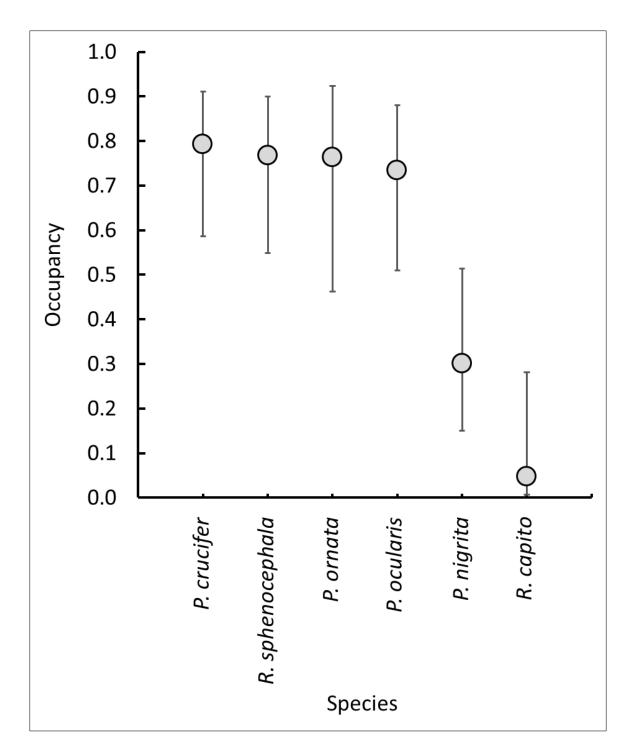


Figure 2.6: Estimates for species occupancy rates and 95% confidence intervals for anurans among 24 Alapaha River Wildlife Management Area ponds.

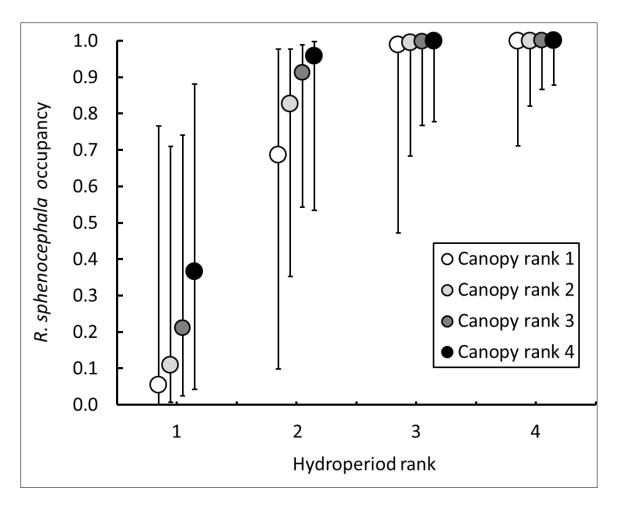


Figure 2.7: Occupancy estimates and 95% confidence intervals for *R. sphenocephala* as predicted by hydroperiod rank and canopy cover rank (Model 4; Table 2.2). Canopy cover rank within the pond: $1 = \langle 25\%, 2 = \langle 50\%, 3 = \langle 75\%, 4 = \rangle 75\%$. Hydroperiod rank: 1 = no water present in 2017, 2 = 30-90 days, 3 = 90-180 days, 4 = >180 days.

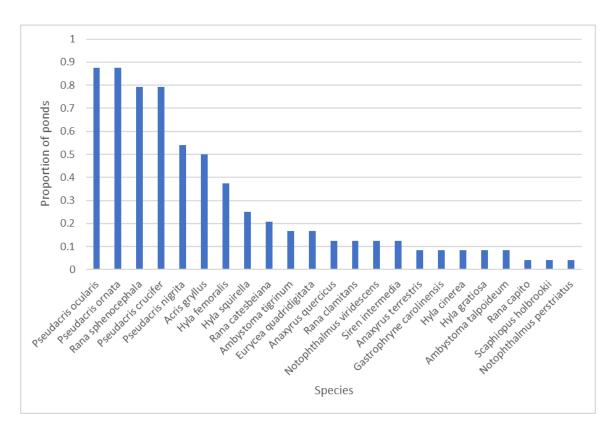


Figure 2.8: Proportion of 24 ponds occupied by anuran and caudate species between December 2016 and June 2017. A species is recorded as present at a pond if any life stage of the species was documented on any sampling occasion and by any detection method employed in these surveys.

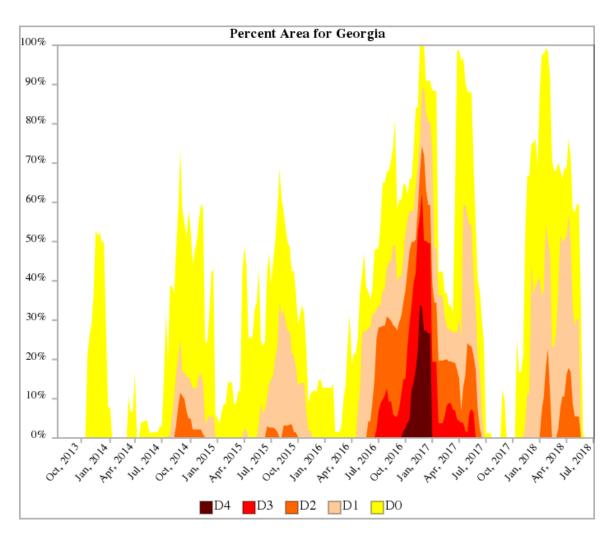


Figure 2.9: Percent area in Georgia experiencing drought in 2013-2018. Pond and amphibian surveys conducted December 2016-June 2017 at Alapaha River WMA followed an extended period of drought in South Georgia, and precipitation in winter and spring of 2017 failed to recharge many pond basins. The five levels of drought intensity, DO, D1, D2, D3, and D4, correspond to abnormally dry, moderate drought, severe drought, extreme drought, and exceptional drought conditions (US Drought Monitor, National Drought Mitigation Center, United State Department of Agriculture and National Oceanographic and Atmospheric Association 2018).

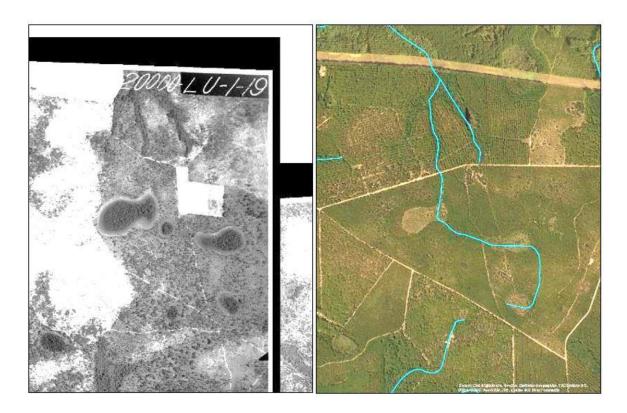


Figure 2.10: A 1937 aerial photograph of ponds at Alapaha and current conditions with ditching connecting ponds 8, 9, 10, and 20 (highlighted by the NHD flowline in the image on the right) (Google Earth imagery 2018).

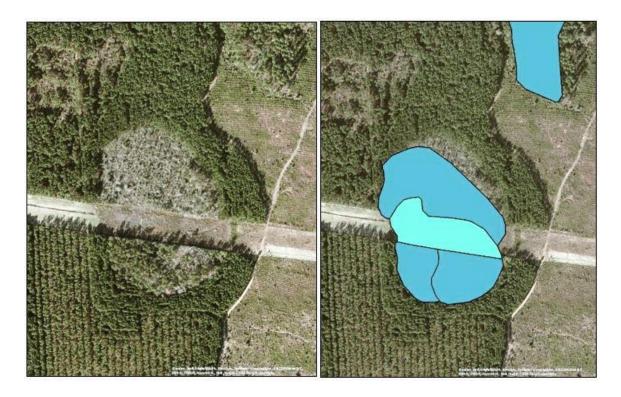


Figure 2.11: The pond where Gopher frogs were detected at Alapaha River WMA and the different wetland classifications represented by the National Wetland Inventory. A powerline right of way transforms a 7.28-ha forested wetland, creating a linear, 1.36-ha emergent, herbaceous wetland through the center (Google Earth imagery 2018).



Figure 2.12: An adult Striped newt (Notophthalmus perstriatus) found at pond 18.

CHAPTER 3

ESTIMATION OF WETLAND HYDROPERIODS USING LANDSAT AND DYNAMIC SURFACE WATER EXTENT (DSWE) DATA

Introduction

Wetland hydroperiod is an important determinant of population dynamics and community composition for pond-breeding amphibians (Pechmann, Scott, Whitfield Gibbons, & Semlitsch, 1989; Snodgrass, Komoroski, Jr, & Burger, 2000; Babbitt, 2005; Baldwin, Calhoun, & deMaynadier, 2006; Matthews, Funk, & Ghalambor, 2013; S. M. Amburgey, Bailey, Murphy, Muths, & Funk, 2014; Pilliod, Arkle, Robertson, Murphy, & Funk, 2015; Greenberg, Zarnoch, & Austin, 2017). Hydroperiod is a large determinant of wetland productivity and resources as well as predator abundance and composition (Gregoire & Gunzburger, 2008; S. Amburgey, Funk, Murphy, & Muths, 2012; S. M. Amburgey et al., 2014). Generally, as wetland hydroperiod increases, so does the likelihood that the wetland will support fish and other predators of amphibian eggs and larvae. Shorter-hydroperiod wetlands, particularly that have open canopies, are more likely to have dense herbaceous communities and sufficient light, so are often more productive in addition to having fewer predators. However, shorter-hydroperiod wetlands have higher risks of early drying and catastrophic larval mortality. As a result, amphibians trade off resource availability and the risk of wetland drying against predator vulnerability, and species are often differentially adapted to persist among wetlands within a particular range of hydroperiods (Snodgrass, Komoroski, et al., 2000; Babbitt,

Baber, & Tarr, 2003). Amphibian species that exhibit rapid development may exploit wetlands with short hydroperiods, while species with stronger antipredator defenses and slower rates of larval development may utilize ponds with more permanent hydroperiods. Positioned somewhere in the middle of that gradient, wetlands with intermediate or semipermanent hydroperiods (i.e., wetlands that dry at least every few years) can promote increased amphibian species richness and diversity by mediating threats of desiccation or increased predation associated with the more extreme ends of the spectrum. For a species such as the Gopher frog (*Rana capito*), which exhibits fewer antipredator defenses relative to other Ranids and has a larval period of 100-210 days post hatch, isolated wetlands with intermediate hydroperiods may be critical to recruitment success and population persistence (Semlitsch, Gibbons, & Tuberville, 1995; Palis, 1998; Gregoire & Gunzburger, 2008; S. M. Amburgey et al., 2014).

The need to integrate information on wetland hydroperiods to identify and manage important habitats is more critical in the face of climate change. Climate projections for the southeastern United States suggest that hydroperiods will become shorter under climate-induced droughts and altered weather patterns, and that pondbreeding amphibians in many coastal plain ecosystems with numerous isolated wetlands will be negatively impacted (Bates, Kundzewicz, Wu, & Palutikof, 2008). Insufficient hydroperiods, concurrent with periods of increased drought frequency, have long been implicated in declines in reproductive effort (i.e., egg masses, larvae, or calling) and population size for many at-risk pond-breeding amphibian species (Pechmann et al., 1989; P. Daszak et al., 2005; Greenberg, Goodrick, Austin, & Parresol, 2015; Greenberg et al., 2017). A 2016 study combined historic climate data and long-term monitoring to

hindcast wetland hydroperiods and concluded that, over the past century, average hydroperiod for ephemeral wetlands in Florida's panhandle was shortest from 1999–2014 (Chandler, Rypel, Jiao, Haas, & Gorman, 2016). The frequency and severity of drought projected for the southeastern U.S. would limit the number of years in which wetland hydroperiods are suitable for reproduction for many pond-breeding amphibians with longer larval development periods.

It is clear that measurements of wetland hydroperiod are important metrics to include in habitat suitability and population models for aquatic-breeding amphibian species, but conventional methods for categorizing wetlands by hydroperiod are timeand labor-intensive. A wetland's hydroperiod varies from year to year and is dependent on a wetland's size, geomorphology, vegetation, soils, groundwater connectivity, and annual variation in temperature, precipitation, timing of rainfall, and human modifications (Babbitt & Tanner, 2000; Snodgrass, A. Lawrence Bryan, & Burger, 2000; Snodgrass, Komoroski, et al., 2000; Brooks, 2005). Trends in wetland hydroperiods may become apparent only after many years, perhaps decades, of close monitoring (Snodgrass, Komoroski, et al., 2000; Skidds & Golet, 2005; Diaz-Delgado et al., 2016; Riley, Calhoun, Barichivich, & Walls, 2017). Conventional methods of monitoring water levels and pond hydroregimes are burdensome, often requiring costly installation or operation of wells or daily visits to check staff gauges (Buchanan & Somers, 1982; McCobb, LeBlanc, & Socolow, 1999). Common wetland inventory and classification techniques currently in use include on-site evaluations, aerial photo interpretation, and digital image processing, but these techniques, without sufficient replication over time, do not capture the dynamic nature of inundation within wetland basins (Baker, Lawrence, Montagne, & Patten, 2006). Newer technologies in monitoring surface water and inundation patterns in wetlands have been developed, but these, too, require a large investment in time before patterns emerge and provide no means for assessing historic hydroperiods (Anderson et al., 2015). In lieu of more direct estimates of wetland hydroperiod, wetland area has been used as a surrogate metric, but wetland area is not a strong correlate with hydroperiod for many types of wetlands across the southeastern U.S.

Remote sensing presents an alternative to more intensive field methods for estimating hydroperiods. Remote sensing has been used to produce high-resolution mapping of land and water across the globe, but dynamically changing systems such as wetlands often require finer resolution temporal and spatial data than are readily available to identify the patterns which define these systems (Pekel, Cottam, Gorelick, & Belward, 2016). As a result, seasonally inundated wetlands, particularly geographically isolated wetlands because of their lack of significant surface water connections, are notably underestimated or misrepresented in national mapping databases (Leonard, Baldwin, Homyack, & Wigley, 2012; Martin, Kirkman, & Hepinstall-Cymerman, 2012; Pitt et al., 2012; Lane & D'Amico, 2016). However, new methodologies developed using freely available Landsat data are being tested in efforts to identify and map these unique dynamic wetland resources (Baker et al., 2006; Diaz-Delgado et al., 2016; Dvorett, Davis, & Papes, 2016; DeVries et al., 2017). The United States Geological Survey (USGS) has been developing products to address some of these issues relating to mapping dynamic systems, and a new line of data products designed to identify surface water dynamics is currently undergoing testing and validation. Dynamic Surface Water

Extent (DSWE) data products recently have been developed to monitor hydrological processes by detecting the temporal and spatial extent of surface water inundation for dynamic water resources (J. W. Jones, 2015). These products, which rely on an algorithm to estimate subpixel water fraction (SWF), are generated from 30m Landsat imagery (U.S. Geological Survey, 2018). The development and refinement of DSWE products for public use is ongoing, and multiple studies have been conducted to test their accuracy and feasibility for use in monitoring inundation patterns. These exploratory studies have been conducted in several systems, including the dynamic and heterogeneous marshes and sawgrass prairies of the Everglades, Alaska's remote Yukon River, the hardwoodforested Delmarva bay wetlands along the Atlantic coastal plain, and the numerous prairie pothole wetlands that freckle the Great Plains of Canada and the northwestern U.S.(J. W. Jones, 2015; DeVries et al., 2017; Bjerklie et al., 2018). Efforts to identify and minimize errors and increase accuracy are underway in these systems, but DSWE data products have not yet been tested in isolated wetlands embedded in pine forests and savannas of the southeastern U.S.

The objective of this study was to determine if DSWE data products could be used to estimate hydroperiods for ponds at the Alapaha River Wildlife Management Area (ARWMA) in Irwin County, Georgia (see Chapter 1: Study Area), which is a site managed for several conservation priority species including the Gopher frog and Striped newt (*Notophthalmus perstriatus*). Both of these species are candidates for federal protection under the Endangered Species Act, and the identification and preservation or restoration of ponds with intermediate to semipermanent hydroperiods is likely critical to increasing population persistence. In the study area, depressional wetlands are generally

inundated following rain events occurring in winter and spring. Average annual precipitation is 47.3 inches, and, while the area experiences high variability in monthly rainfall, the 31 days centered around March 2 represent a time of peak rainfall, with an average of 4.6 inches reported during that timeframe (Weatherspark.com, 2018). Drying dates vary with annual fluctuations in precipitation and temperature, but most ephemeral depression wetlands will dry between spring or early fall in this region; the wetlands will experience increased rates of drying following spring leaf-out. The development of an efficient technique to remotely assess wetland hydroperiod would be valuable for the development of habitat suitability models and habitat management plans for these and other wetland species. My specific objectives were to (1) determine whether DSWE data products can be used to detect surface water within forested and open canopy wetlands at ARWMA, (2) automate a process to identify annual inundation patterns for a series of wetlands across a landscape, and (3) estimate hydroperiod trends for all isolated wetlands at ARWMA.

Methods

ARWMA wetland hydroperiod field surveys

Seasonal flooding and drying regimes were recorded for 24 ponds across Alapaha River Wildlife Management Area using eight standardized field surveys from December 2016 through June 2017. I used NWI geospatial data and the Georgia Department of Natural Resources' wetland layer for ARWMA to select sites to visit and then groundtruthed the sites in the fall of 2016, when most ponds were dry, by confirming the

presence of crayfish burrows (active or inactive) or plants with wetland designations (Tiner, 1993).

Upon each visit, ponds were recorded as either wet or dry, and maximum water depth was recorded on each visit. In the case where a wetland's maximum water depth was extremely shallow, <5 cm, or isolated to a very small pool, a narrow ditch, or a stumphole, ponds were recorded as wet, but notes about the observed limited extent of water were recorded as well. When possible, filling dates and drying dates were estimated based on these field surveys, and the number of consecutive occasions wherein ponds held water were recorded, as well.

Field observations of pond hydroperiods for 2016-2017

While surface water in ditches or puddles may be biologically relevant to amphibians, these features would not be expected to appear in DSWE data with 30m resolution pixels. Further, a wetland with < 5 cm of water at its maximum depth may be observed as wet during a survey but was likely dry within a few days. I reclassified my "wet" values so that I could interpret likely drying events between surveys. This reclassified table was also used to account for several scenarios in which DSWE data would be unable to detect surface water recorded in ponds during site visits. For each date, a pond with a maximum water level exceeding 15 cm was recorded as Deep; a pond with maximum water levels between 5 and 15 cm was recorded as Shallow; and a pond with a maximum water level of less than 5 cm was recorded as Drying. In addition, if the surface water recorded for a pond was restricted to a narrow, linear ditch or a puddle or sinkhole within the basin, an asterisk (referencing a "puddle or ditch") was added next to the value of Deep, Shallow, or Drying for that date.

Dynamic Surface Water Extent data acquisition

Dynamic Surface Water Extent (DSWE) data products were made available for use in this analysis by USGS researcher Dr. John Jones (Landsat Level 3 Dynamic Surface Water Extent (DSWE) Science Products, courtesy of the U.S. Geological Survey). This provisional data set includes DSWE interpretations of imagery that was acquired by Landsat 7 and Landsat 8 satellites from March 2013 through March 2018. The Operational Land Imager (OLI) instrument onboard the Landsat 8 satellite uses 9 spectral bands to acquire 30-meter-resolution images of the Earth on a 16-day cycle; an algorithm had been previously applied to these images to estimate the extent of surface water present at discrete points in time (J. W. Jones, 2015). Landsat 7 and Landsat 8 orbits are offset by 8 days, allowing for more repeat coverage. Landsat 7 TM DSWE imagery was used to supplement the data set when suitable Landsat 8 OLI imagery was unavailable. The algorithm used to produce these DSWE products can be found in the appendix (Appendix 3.1). When released to the public, the DSWE data products will provide six raster layers: a diagnostic layer, an interpreted layer, a mask layer, an interpreted layer with a mask applied, a hillside layer, and a percent slope layer (U.S. Geological Survey, 2018).

Prior to downloading data from the DSWE data set, I evaluated scene cloud cover at www.earthexplorer.usgs.gov for all available Landsat 8 scenes between 01 January and 30 June (2015, 2016, 2017) for path 38, row 180. This timeframe of January through June corresponded to my field surveys in 2017 and the window when many focal amphibian species breed and complete their larval development. I excluded images with >80% cloud cover from my analysis.

I reviewed several scenes to compare the interpreted layer and the interpreted-masked layer, as was recommended by the author of the DSWE algorithm (John Jones, U.S. Geological Survey, pers. comm.). Due to frequent overprediction of clouds within the mask layer, the interpreted layer was selected for use in the analysis. For 2015, DSWE data from Landsat 8 was downloaded for eight scenes from January through June, but two scenes were not included due to the cloud cover that amassed over the study area obscuring most of the study ponds. For 2016, DSWE data was downloaded for seven scenes. For 2017, DSWE data was downloaded for seven scenes (Table 3.1). Four scenes with DSWE data from Landsat 7 were used to supplement Landsat 8 data when extensive cloud contamination prevented its inclusion.

Assessing DSWE estimates for Alapaha wetlands in 2017

Several DSWE scenes were included in a preliminary review to visually evaluate how the DSWE layer interpreted known features and vegetative communities at Alapaha (Figure 3.1, Figure 3.2). Using DSWE scenes and hydroperiod records collected for ARWMA study ponds (Chapter 2), I used a visual assessment to compare DSWE pixel values assigned by the DSWE algorithm with known features of the study area, including ephemeral ponds, permanent impoundments, hardwood forest, pine forest, the river and its floodplain, and open grasslands. Of the six DSWE values, Partial Water—

Conservative most closely corresponded to pixels with mixtures of water and vegetation, as would be seen in most seasonal wetlands at the Alapaha River WMA study site (U.S. Geological Survey, 2018) (J. Jones, U.S. Geological Survey, pers. comm.).

DSWE scenes for 7 dates in 2017 and a shapefile for discrete wetlands [i.e., cypress-gum ponds, herbaceous ponds, and artificial ponds] at Alapaha were compared

using ArcGIS software (ArcGIS 10.4). For each pond, any pixels that were assigned DSWE values of Partial Water—Conservative (PC), Partial Water—Liberal (PL), Not Inundated (NI), and Cloud, Shadow or Snow (C), were noted. These four DSWE pixel values were the only values of interest in identifying surface water presence in ARWMA wetlands. Values of Open Water were disregarded as they represented deeper, more permanent water and reflected aquatic conditions without emergent, floating, or submergent vegetation that is found in wetlands. While some impoundments which were included as study ponds included pixels with these Open Water values, pixels with Partial Water values also occurred along the pond perimeter and, as water levels lowered, throughout the basin as well.

Model to automate process to extract DSWE values for wetlands at Alapaha

In ArcGIS, I used Model Builder to iterate through the selected DSWE imagery and reclassify pixel values into two classes. All pixels which DSWE interpreted as PC, the value best representing surface water presence within seasonal ponds, were coded as 1, and all other pixels were coded as 0.

A second iterative model combined the ARWMA wetland layer with the reclassified DSWE imagery and reported the number of pixels with values of 1 that were found within ponds for each of the dates for which DSWE imagery was included. This process was completed first for 2017 so that results could be compared with field data and then for years 2016 and 2015. A total of 16 DSWE scenes were included in the analyses to represent inundation patterns at ARWMA ponds between January and June of 2015 and January and June of 2016 (Table 3.1). For each year, I exported a table that included the number of pixels with a value of 1 that occurred within each pond. If a pond

had any pixels with a value of 1 with individual DSWE scenes, the pond was coded as "1" for that scene, indicating the DSWE algorithm predicted surface water as present within that pond on the date that DSWE scene was collected.

Comparison of field survey data and data from DSWE analysis

For each study pond, the observed-groundtruthed condition (wet or dry) and the DSWE-predicted condition (wet or dry) were recorded for seven surveys and scenes, respectively. The tabulation of agreement between inundation condition predicted by the DSWE analysis and those observed values reported from groundtruthing is a standard measure of algorithm performance (J. W. Jones, 2015). This metric is termed "agreement" and was measured for the seven scenes/surveys which comprised the 2017 data set. Each DSWE scene collection date was paired with a field survey date within 16 days of the DSWE scene. For each of the 24 study ponds, I extracted seven values of either 1 (wet) or 0 (dry) from the seven DSWE scenes which corresponded to the seven field survey dates where ponds were recorded as wet or dry. This string of values was produced to represent DSWE predictions for each pond's inundation pattern from January through June of 2017 (Table 3.4). For each of these paired sets of dates, I calculated the number of ponds which were recorded as wet during my field observations and the number of ponds predicted as wet from my DSWE data set. For my field observations, I calculated the number of inundated ponds using a reclassified table, which accounted for limited surface water (i.e., shallow or drying conditions, puddles, or ditches). In this table, only values recorded as "deep," or > 5 cm, were classified as Wet. Any other value, including "shallow," "drying," or "deep*" (representing a puddle or ditch with deep water), was reclassified as Dry. I compared the two data sets using

confusion matrices to classify true positives, false positives, true negatives, and false negatives (Fielding & Bell, 1997).

Estimating all Alapaha wetland hydroperiods with DSWE data

Field data collected from one year of wetland surveys is unlikely to be representative of the average hydroperiod of that wetland or of a network of wetlands. Identifying inundation patterns and long-term hydroperiod trends in wetlands can help determine how likely that site may be to support populations of pond-breeding amphibians over time. I used the DSWE data to model predictions for the previous two years of hydrodynamics for wetlands at ARWMA. While no observed data are available for comparison, DSWE data for years 2015 and 2016 were also downloaded and interpreted to determine if DSWE predictions could identify 1) trends in hydroperiod and 2) surface water dynamics at ponds throughout the property.

Using the automated DSWE analysis, I hindcasted estimates for each pond at Alapaha in 2015, 2016, and 2017. Again, any pond with a single pixel value of PC was coded as 1, or "wet," on the date for which that scene was collected. DSWE predictions of wet or dry were calculated for each pond using 9 scenes in 2015, 7 scenes in 2016, and 8 scenes in 2017. These scenes were collected from January through June to represent patterns of seasonal filling of wetlands in the study area as well as the time of year when Gopher frogs require wetlands to have water.

Results

ARWMA study pond hydroperiods from field surveys Dec 2016–Jun 2017

Of the 24 ponds sampled, 5 were dry during all site visits from December 2016 through June 2017 (Table 3.2). Of the 19 ponds which were inundated for some duration of this period, only 3 held some water during all visits; 1 for 6 of 7 visits; 3 for 5 visits, and 1 for 4 visits. There were 11 ponds which held water for only 1 or 2 visits. Of the 3 ponds which held water for all visits from December 2016 through June 2017, one was never dry, from the earliest site visits in October or on any subsequent visit through June 2017 (Table 3.2). The other two ponds that were wet during all visits within the study window were dry in the months prior to the survey period, and one of those ponds was dry a month after my last visit included in this study. Many ponds which were recorded as wet experienced only partial inundation of their basins (Ponds 1, 2, 8, 10, 18, 23, 29, 30, and 41) with water standing longest in deeper parts of the basin, including ditches and ruts (Ponds 1, 2, 3, 4, 8, and 10) (Chapter 2, Figure 2.3, Table 3.2).

Comparison of field survey data and data from DSWE analysis

Between observed conditions and DSW predicted conditions of inundation in ARWMA wetlands, errors of commission were 0, meaning that no wetlands that were dry were ever incorrectly classified as wet by DSWE, but errors of omission were high for predicting which wetlands were inundated at various points in time throughout the study (Table 3.3). Groundtruthed data included 111 records of ponds being dry, and DSWE predictions agreed these 111 records. However, the groundtruthed data included 57 records of ponds having surface water present during field surveys, but DSWE estimates only agreed for 19 of these records. Differences between observed and predicted values

for wetland conditions indicate that DSWE estimates consistently underpredict the number of wetlands with surface water present (Figure 3.3).

Influence of pond attributes on DSWE detection

The accuracy of DSWE estimates varied according to pond characteristics. The estimates were most accurate for nonlinear bodies of water larger than 0.80 ha and with longer or permanent hydroperiods and open canopies (Figure 3.4). Pond 11, a 0.48-ha pond, was too small and unable to be evaluated using DSWE data. Other small ponds were included in the analysis, but, for wetlands which were <0.80 ha in size (24 and 45) or for wetlands with flashier hydroperiods of less than three months (8, 10, 15, 20, 23, 25, 29, 41), surface water could not be reliably detected with DSWE data products (Figure 3.4). The reclassified table of field observations was developed to account for the anticipated inability of the DSWE technique to detect surface water in ditches and puddles, but other unanticipated linear arrangements of surface water were also not detected by DSWE. Several ponds (1 and 2, for example) exceeded 0.80 ha and were recorded as wet during groundtruthing, but still no surface water was detected for either site in the analysis. While surface water was present in these wetlands for months at a time, the surface water was restricted to small or linear features of lower topography within the basin, including ditches, tire ruts, continuously winding game trails, or small borrow pits. In general, the DSWE analysis failed to detect surface water in ponds with flashy hydroperiods, where surface water had been recorded in the field on 3 or fewer site visits (Figure 3.4).

The DSWE analysis detected surface water presence with greater accuracy at ponds with longer hydroperiods, including the single site where Gopher frogs were

detected, a 1.3-ha emergent herbaceous wetland; DSWE predictions agreed with field observations for five out of seven records. Accuracy was highest among open canopied semi-permanent-to-permanent ponds, but surface water was also detected in pine embedded wetlands with 50–75 % canopy cover (Figure 3.4).

Model to automate process to extract DSWE values for wetlands

Two iterative models developed in ModelBuilder in ArcGIS were used to identify pixels that the DSWE algorithm interpreted as a mixture of water and vegetation, as would be seen in shallow, ephemeral wetlands. These pixel values were reclassified to either 1 (PC value) or 0 for nine scenes in 2015, seven scenes in 2016, and eight scenes in 2017. The second model combined the reclassified DSWE data with the Alapaha wetland layer which included 53 ponds. For each pond, the model iterated through each reclassified DSWE scene and identified any pixel or cluster of pixels with a value of 1. For each year, I exported a table which included the number of pixels with a value of 1 that occurred within each pond. If a pond had any pixels with a value of 1 in a specific DSWE scene, the pond was coded as "1," meaning that it likely had surface water present on the date that DSWE scene was collected. Wetland hydroperiods were recreated using individual pond histories of "1"s and "0"s (Table 3.4, Table 3.6, Table 3.7). See appendix for extraction and export steps completed in ArcGIS.

Estimating all Alapaha wetland hydroperiods with DSWE data

The automated model was used to create tables presenting strings of 1s and 0s, representing DSWE predictions for inundation patterns in ARWMA wetlands for January through June of 2015, 2016, and 2017 (Table 3.4, 3.6, and 3.7). Similar patterns of filling

and drying could be observed between years, but with each year, DSWE predicted fewer wetlands with surface water present from January through June than I observed in the field.

Discussion

The study area including ARWMA experienced D4 exceptional drought conditions throughout the fall of 2016 (Chapter 2, Figure 2.9), following a summer with less severe D3 and D2 drought classifications (USDM, 2018). Winter precipitation levels in 2017 exceeded average precipitation levels for the area, but previous months of drought likely slowed the rate of wetland recharge (USGS 2017). Many wetlands did not fill, and my data set for comparison was too small to quantitatively assess the predictive power of the DSWE analysis for different types of wetlands. Even so, my preliminary findings suggest that several wetland characteristics may influence DSWE's ability to detect surface water in wetlands. In small ponds < 0.80 ha, DSWE often failed to detect surface water. Ponds 45 and 24 had long hydroperiods and were observed wet on each of seven field surveys, but DSWE predicted both ponds as dry for all seven scenes corresponding to those 2017 surveys. Pond 45 is a 0.38-ha open-canopy borrow pit that was likely permanent and unsuitable for Gopher frogs; fish were detected on most surveys (Chapter 2, Table 2.3). In addition to its small size, it is linear in shape, another factor which may limit surface water detection with DSWE data. Pond 24 is a 0.65-ha, fishless, cypress-gum pond with less than 50 % canopy cover that was occupied by at least fourteen species of amphibians based on 2016-2017 sampling. Ponds as small as 0.3 ha can be ecologically important and support rich amphibian assemblages, but these

omissions suggest that many small wetlands with suitable hydroperiods may by overlooked by the DSWE algorithm (Semlitsch and Bodie, 1998; Snodgrass, Komoroski, et al., 2000).

Wetland vegetation, canopy cover, and length of observed hydroperiod also appeared to influence DSWE predictions for surface water presence. DSWE predictions were able to detect water in open canopied wetlands [exceeding 0.80 ha in size] and in wetlands with up to 75 % canopy cover, but less likely to detect water in those wetlands where shorter, flashier hydroperiods were observed (Figure 3.6). For pond 18, for which surface water was detected with DSWE data in only 25% of the occasions where groundtruthing had determined it was wet, the spectral signature of the dense sphagnum mat which covered the shallow basin may have interfered with the interpretation of surface water presence (J. Jones, U.S. Geological Survey, pers. comm.).

Based on the high number of omission errors in my original DSWE analysis, I knew that I would be unable to accurately predict pond filling and drying for all of the Alapaha wetlands using DSWE data products. However, the amount of agreement I found between DSWE predictions and actual observations for some of the ponds in that preliminary analysis suggests that DSWE data products may be useful for detecting surface water in a subset of ponds: those that were greater than 0.80 ha in size and with hydroperiods of intermediate to semipermanent or permanent length. The DSWE algorithm may be used to identify these ponds, which, given their hydroperiods, may be most likely to provide suitable conditions for Gopher frogs. Of note, the DSWE analysis detected surface water presence with greater accuracy at the single site where Gopher frogs were detected, a 1.37-ha emergent herbaceous wetland which occurs within a

powerline right of way; DSWE predictions agreed with field observations on five out of seven occasions.

Ponds with the longest predicted hydroperiods in 2017 were also predicted to have the longest hydroperiods in 2015 and 2016 (Table 3.4, 3.6, 3.7). Five of the nine ponds with the consistently longest hydroperiods are artificial ponds, with most of them supporting predatory fish populations or being otherwise unsuitable for Gopher frogs. While the DSWE predictions underestimate the duration of hydroperiods, this exercise suggests that Alapaha has very few larger natural ponds with intermediate-to-semipermanent hydroperiods.

A comparison of DSWE predictions for the number of ponds at Alapaha with surface water present in 2015, 2016, and 2017 suggests that, with each year, Gopher frogs would have found fewer and fewer ponds which held water through May or June, a commonly reported time of metamorphosis for Georgia populations of Gopher frogs. The number of ponds with available surface water in May and June decreased from 2015 to 2016 to 2017, with only four ponds predicted to have water in June of 2017. Of these four ponds, only two could likely support Gopher frogs, as the other two ponds are more permanent in nature and support populations of predatory fish. Given the spatial pattern of drying which occurs in seasonally inundated wetlands, where water persists in puddles or shrinking pools, the DSWE technique likely still underestimates the number of ponds which are wet enough for amphibian larvae to survive through late spring and early summer; ponds which are predicted to have dried in April may actually hold water long enough in portions of their basins to support recruitment.

DSWE data would benefit from continued testing in a variety of vegetative and aquatic communities occurring throughout the southeastern U.S. While direct measurements using DSWE data currently may be of limited use for estimating hydropatterns in some types of aquatic systems, DSWE imagery can provide a useful data set for researchers or conservation managers seeking to identify wetlands with intermediate to semi-permanent hydroperiods.

While this analysis focused at the level of pond hydrodynamics, the surrounding terrestrial landscape, and the conversion to and management of upland pine forests, have likely interfered with historic inundation patterns of wetlands at Alapaha (McCauley, Anteau, Post van der Burg, & Wiltermuth, 2015). Modification of wetlands was common across Alapaha, with some ponds created from stream impoundments or borrow pits and natural ponds altered by connective ditches, encircled by deeply ditched fire breaks, or overplanted with slash pine edging into the pond basin (See Chapter 1). In addition, forestry practices which increase the basal area of slash pine in the immediate uplands and into the ecotone of embedded wetlands intercept precipitation which would otherwise feed depression wetlands (Bosch & Hewlett, 1982; Bryant, Bhat, & Jacobs, 2005; C. N. Jones, McLaughlin, Henson, Haas, & Kaplan, 2018). This reduced availability of water, combined with the more direct physical changes to pond basins, are likely to have altered the hydrology of these ponds by reducing the depth of wetlands, the duration of wetland hydroperiods, and the impermeability of the wetland basins. Degradation and modification of wetlands and uplands influence the surface water availability within ponds at Alapaha, but their impacts are difficult to isolate from those impacts caused by many interacting and stochastic environmental factors, particularly in a year following a

period of extended drought conditions. It seems likely, however, that the capacity of Alapaha ponds to hold water has been reduced by these land use practices.

With anticipated impacts from climate change, southeastern wetland communities are expected to undergo increased variability in precipitation and increased rates of evaporative water loss, and efficient methods of tracking these shifts will become increasingly important. Impacts to pond hydrology or holding capacity will be amplified under these predicted scenarios. The DSWE data products may provide us with a valuable tool for monitoring long-term trends in wetland hydroperiods and for identifying changes in wetland hydropatterns that may result from upland or wetland management.

Literature Cited

- Amburgey, S., Funk, W. C., Murphy, M., & Muths, E. (2012). Effects of hydroperiod duration on survival, developmental rate, and size at metamorphosis in boreal chorus frog tadpoles (*Pseudacris maculata*). *Herpetologica*(4), 456.
- Amburgey, S. M., Bailey, L. L., Murphy, M., Muths, E., & Funk, W. C. (2014). The effects of hydropattern and predator communities on amphibian occupancy. *Canadian Journal of Zoology*, 92(11), 927-937. doi:10.1139/cjz-2014-0106
- Anderson, T. L., Heemeyer, J. L., Peterman, W. E., Everson, M. J., Ousterhout, B. H., Drake, D. L., & Semlitsch, R. D. (2015). Automated analysis of temperature variance to determine inundation state of wetlands. *Wetlands Ecology and Management*(6), 1039. doi:10.1007/s11273-015-9439-x
- Babbitt, K. J. (2005). The relative importance of wetland size and hydroperiod for amphibians in southern New Hampshire, USA. *Wetlands Ecology and Management*, 13(3), 269.
- Babbitt, K. J., Baber, M. J., & Tarr, T. L. (2003). Patterns of larval amphibian distribution along a wetland hydroperiod gradient. *Canadian Journal of Zoology*(9), 1539.
- Babbitt, K. J., & Tanner, G. W. (2000). Use of temporary wetlands by anurans in a hydrologically modified landscape, *Wetlands* 20: 313–22.
- Baker, C., Lawrence, R., Montagne, C., & Patten, D. (2006). Mapping wetlands and riparian areas using Landsat ETM+ imagery and decision-tree-based models.

- Wetlands, 26(2), 465-474. doi:10.1672/0277-5212(2006)26[465:MWARAU]2.0.CO;2
- Baldwin, R. F., Calhoun, A. J. K., & deMaynadier, P. G. (2006). The significance of hydroperiod and stand maturity for pool-breeding amphibians in forested landscapes. *Canadian Journal of Zoology*(11), 1604.
- Bates, B. C., Kundzewicz, Z. W., Wu, S., & Palutikof, J. P. (2008). *Climate Change and Water* In Intergovernmental Panel on Climate Change (Ed.), *IPCC Technical Paper VI*.
- Bjerklie, D. M., Birkett, C. M., Jones, J. W., Carabajal, C., Rover, J. A., Fulton, J. W., & Garambois, P.-A. (2018). Satellite remote sensing estimation of river discharge:
 Application to the Yukon River Alaska. *Journal of Hydrology*, 561, 1000-1018.
 doi:10.1016/j.jhydrol.2018.04.005
- Bosch, J. M., & Hewlett, J. D. (1982). A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology*, 55(1-4), 3-23.
- Brooks, R. (2005). A review of basin morphology and pool hydrology of isolated ponded wetlands: implications for seasonal forest pools of the northeastern United States.

 Wetlands Ecology & Management, 13(3), 335-348. doi:10.1007/s11273-004-7526-5
- Bryant, M. L., Bhat, S., & Jacobs, J. M. (2005). Measurements and modeling of throughfall variability for five forest communities in the Southeastern US. *Journal of Hydrology*, 312(1-4), 95-108. doi:10.1016/j.jhydrol.2005.02.012

- Buchanan, T. J., & Somers, W. P. (1982). Stage Measurements at Gaging Stations. In U.S. G. Survey (Ed.), U.S. Geological Survey Techniques of Water-ResourcesInvestigations Book 3 (pp. 28).
- Chandler, H. C., Rypel, A. L., Jiao, Y., Haas, C. A., & Gorman, T. A. (2016).
 Hindcasting Historical Breeding Conditions for an Endangered Salamander in
 Ephemeral Wetlands of the Southeastern USA: Implications of Climate Change.
 PLoS ONE, 11(2), 1-17. doi:10.1371/journal.pone.0150169
- DeVries, B., Huang, C., Huang, W., Lang, M. W., Jones, J. W., Creed, I. F., & Carroll,
 M. L. (2017). Automated Quantification of Surface Water Inundation in Wetlands
 Using Optical Satellite Imagery. *Remote Sensing*, 9(8).
- Diaz-Delgado, R., Bustamante, J., Diaz-Delgado, R., Aragones, D., Afan, I., &

 Bustamante, J. (2016). Long-Term Monitoring of the Flooding Regime and

 Hydroperiod of Donana Marshes with Landsat Time Series (1974-2014). *Remote Sensing*, 8(9).
- Dvorett, D., Davis, C., & Papeş, M. (2016). Mapping and Hydrologic Attribution of Temporary Wetlands Using Recurrent Landsat Imagery. *Wetlands*, *36*(3), 431-443. doi:10.1007/s13157-016-0752-9
- Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*(1), 38.
- Greenberg, C. H., Goodrick, S., Austin, J. D., & Parresol, B. R. (2015). Hydroregime Prediction Models for Ephemeral Groundwater-Driven Sinkhole Wetlands: a

- Planning Tool for Climate Change and Amphibian Conservation. *Wetlands*, *35*(5), 899-911.
- Greenberg, C. H., Zarnoch, S. J., & Austin, J. D. (2017). Weather, hydroregime, and breeding effort influence juvenile recruitment of anurans: implications for climate change. *Ecosphere*, 8(5).
- Gregoire, D. R., & Gunzburger, M. S. (2008). Effects of Predatory Fish on Survival and Behavior of Larval Gopher Frogs (*Rana capito*) and Southern Leopard Frogs (*Rana sphenocephala*). *Journal of Herpetology*(1), 97.
- Jones, C. N., McLaughlin, D. L., Henson, K., Haas, C. A., & Kaplan, D. A. (2018). From salamanders to greenhouse gases: does upland management affect wetland functions?, *Frontiers in Ecology and the Environment*, 16(1), 14-19.
- Jones, J. W. (2015). Efficient Wetland Surface Water Detection and Monitoring via Landsat: Comparison with in situ Data from the Everglades Depth Estimation Network. *Remote Sensing*, Vol 7, Iss 9, Pp 12503-12538 (2015)(9), 12503.
- Lane, C. R., & D'Amico, E. (2016). Identification of Putative Geographically Isolated

 Wetlands of the Conterminous United States. *Journal of the American Water*Resources Association(3), 705. doi:10.1111/1752-1688.12421
- Leonard, P. B., Baldwin, R. F., Homyack, J. A., & Wigley, T. B. (2012). Remote detection of small wetlands in the Atlantic coastal plain of North America: Local relief models, ground validation, and high-throughput computing. *Forest Ecology and Management*, 284, 107-115. doi:10.1016/j.foreco.2012.07.034

- Martin, G. I., Kirkman, L. K., & Hepinstall-Cymerman, J. (2012). Mapping
 Geographically Isolated Wetlands in the Dougherty Plain, Georgia, USA.

 Wetlands(1), 149.
- Matthews, J. H., Funk, W. C., & Ghalambor, C. K. (2013). Demographic approaches to assessing climate change impact: an application to pond-breeding frogs and shifting hydropatterns. In J. F. Brodie, E. S. Post, & D. F. Doak (Eds.), *Wildlife Conservation in a Changing Climate* (pp. 58-85). Chicago, Illinois: University of Chicago Press.
- McCauley, L. A., Anteau, M. J., Post van der Burg, M., & Wiltermuth, M. T. (2015).

 Land use and wetland drainage affect water levels and dynamics of remaining wetlands. *Ecosphere*, 6(6).
- McCobb, T. D., LeBlanc, D. R., & Socolow, R. S. (1999). A Siphon Gage for Monitoring Surface-Water Levels, 1141.
- P. Daszak, D. E. Scott, A. M. Kilpatrick, C. Faggioni, J. W. Gibbons, & D. Porter. (2005). Amphibian Population Declines at Savannah River Site are Linked to Climate, Not Chytridiomycosis. *Ecology*(12), 3232.
- Palis, J. G. (1998). Breeding Biology of the Gopher Frog, Rana capito, in Western Florida. *Journal of Herpetology*(2), 217. doi:10.2307/1565300
- Pechmann, J., Scott, D., Whitfield Gibbons, J., & Semlitsch, R. (1989). Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. *Wetlands Ecology & Management*, 1(1), 3.

- Pekel, J. F., Cottam, A., Gorelick, N., & Belward, A. S. (2016). High-resolution mapping of global surface water and its long-term changes. *Nature*, *540*(7633), 418-422. doi:10.1038/nature20584
- Pilliod, D. S., Arkle, R. S., Robertson, J. M., Murphy, M. A., & Funk, W. C. (2015). Effects of changing climate on aquatic habitat and connectivity for remnant populations of a wide-ranging frog species in an arid landscape. *Ecology and Evolution*, *5*(18).
- Pitt, A. L., Baldwin, R. F., Lipscomb, D. J., Brown, B. L., Hawley, J. E., Allard-Keese,
 C. M., & Leonard, P. B. (2012). The missing wetlands: using local ecological knowledge to find cryptic ecosystems. *Biodiversity and Conservation*, 21(1), 51-63.
- Riley, J. W., Calhoun, D. L., Barichivich, W. J., & Walls, S. C. (2017). Identifying Small Depressional Wetlands and Using a Topographic Position Index to Infer Hydroperiod Regimes for Pond-Breeding Amphibians. *Wetlands*, *37*(2), 325-338.
- Semlitsch, R. D. and Bodie, J. R. (1998). Are small, isolated wetlands expendable?

 *Conservation Biology, (12) 5: 1129-1133.
- Semlitsch, R. D., Gibbons, J. W., & Tuberville, T. D. (1995). Timing of Reproduction and Metamorphosis in the Carolina Gopher Frog (*Rana capito capito*) in South Carolina. *Journal of Herpetology*, 29(4), 612-614. doi:10.2307/1564746
- Skidds, D. E., & Golet, F. C. (2005). Estimating hydroperiod suitability for breeding amphibians in southern Rhode Island seasonal forest ponds, *Wetlands Ecology and Management*, 13(3):349-366.

- Snodgrass, J. W., A. Lawrence Bryan, J., & Burger, J. (2000). Development of Expectations of Larval Amphibian Assemblage Structure in Southeastern Depression Wetlands. *Ecological Applications*(4), 1219-1229.
- Snodgrass, J. W., Komoroski, M. J., Jr, A. L. B., & Burger, J. (2000). Relationships among Isolated Wetland Size, Hydroperiod, and Amphibian Species Richness: Implications for Wetland Regulations. *Conservation Biology*, *14*(2), 414-419.
- Tiner, R. W. (1993). Using Plants as Indicators of Wetland. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 240.
- U.S. Geological Survey. (2018). Landsat Dynamic Surface Water Extent (DSWE)

 Product Guide.
- Weatherspark.com. (2018). Average Weather in Ocilla. Retrieved from https://weatherspark.com/y/16209/Average-Weather-in-Ocilla-Georgia-United-States-Year-Round)

Table 3.1: Landsat scenes used in the analyses from 15 January 2015 to 24 June 2017.

Imagery	OLI or ETM Scene	Scene Cloud Cover	
collection			
date			
10-Jan-15	LC08_L1TP_018038_20150110_20170302_01_T1	5.01	
3-Feb-15	LE07_L1TP_018038_20150203_20160903_01_T1_	DSWE download	
7-Mar-15	LE07_L1TP_018038_20150307_20160903_01_T1	DSWE download	
31-Mar-15	LC08_L1TP_018038_20150331_20180130_01_T1	39.29	
2-May-15	LC08_L1TP_018038_20150502_20170228_01_T1	0.1	
8-Apr-15	LE07_L1TP_018038_20150408_20160904_01_T1	DSWE download	
18-May-15	LC08_L1TP_018038_20150518_20170228_01_T1	38.63	
3-Jun-15	LC08_L1TP_018038_20150603_20170226_01_T1	43.13	
19-Jun-15	LC08_L1TP_018038_20150619_20170226_01_T1	8.6	
13-Jan-16	LC08_L1TP_018038_20160113_20170224_01_T1	1.04	
29-Jan-16	LC08_L1TP_018038_20160129_20170224_01_T1	0.02	
14-Feb-16	LC08_L1TP_018038_20160214_20170224_01_T1	36.09	
1-Mar-16	LC08_L1TP_018038_20160301_20170224_01_T1	0.58	
18-Apr-16	LC08_L1TP_018038_20160418_20170223_01_T1	0.01	
4-May-16	LC08_L1TP_018038_20160504_20170223_01_T1	7.71	
21-Jun-16	LC08_L1TP_018038_20160621_20180130_01_T1	7.67	
15-Jan-17	LC08_L1TP_018038_20170115_20170218_01_T1	33.79	
31-Jan-17	LC08_L1TP_018038_20170131_20170218_01_T1	0.02	
16-Feb-17	LC08_L1TP_018038_20170216_20170228_01_T1	0.01	
4-Mar-17	LC08_L1TP_018038_20170304_20170316_01_T1	0.01	
20-Mar-17	LC08_L1TP_018038_20170320_20170328_01_T1	8.15	
21-Apr-17	LC08_L1TP_018038_20170421_20170501_01_T1	2.38	
7-May-17	LC08_L1TP_018038_20170507_20170515_01_T1	0.02	
16-June-17	LE07_L1TP_018038_20170616_20170621_01_T1	DSWE download	

Table 3.2: Reclassified table of field observations of surface water presence in 24 study ponds at Alapaha. Only observations recorded here as "deep" were included in the comparative analysis with DSWE data.

	Survey 1 19-Jan 2017	Survey 2 11-Feb 2017	Survey 3 9-Mar 2017	Survey 4 2-Apr 2017	Survey 5 22-Apr 2017	Survey 6 18-May 2017	Survey 7 18-Jun 2017
45	deep	deep	deep	deep	deep	deep	deep
24	deep	deep	deep	deep	deep	deep	deep
46	deep	deep	deep	deep	deep	deep	deep
2	deep	deep	deep	deep	deep	deep*	
1	deep	deep	deep	deep	shallow		
4	deep	deep	deep	shallow	deep		
3	deep	deep	deep	deep	deep		
30	deep	deep	deep	deep			
42	NA	deep	deep				
18	drying	deep	deep	drying*			
31	deep	deep	shallow				
15		shallow	shallow	drying	8		
8	drying	deep	deep				
10		deep	deep*				
25	deep	shallow	drying				
41	drying	deep	drying*				
20		shallow					
23		deep	shallow*				
29		shallow					
14							
36				5.5			10
44	3			\$			
43	3	*					13
35							
	70	30	₹.	*			*
					no water/dry <5 cm 5–15 cm		
				drying			
				shallow			
				deep	>15 cm		
				*	water limited to puddle / ditch		

Table 3.3: The wettest DSWE pixel values that were found within each wetland from seven scenes collected from January through June of 2017.

Pond #	Scene 1	Scene 2	Scene 3	Scene 4	Scene 5	Scene 6	Scene 7		
	31-Jan	16-Feb	4-Mar	20-Mar	21-Apr	7-May	16-Jun		
	2017	2017	2017	2017	2017	2017	2017		
45	PL	PL	NI	NI	NI	NI	PL		
24	NI	NI	PL	PL	NI	PL	PL		
46	PC	PC	PC	PC	PC	PC	PC		
2	PL	NI	PL	PL	PL	NI	NI		
1	NI	NI	NI	NI	PL	NI	NI		
4	PC	PL	PC	PL	NI	NI	NI		
3	PC	PL	PC	PC	NI	NI	PL		
30	PC	PC	PC	PC	NI	NI	NI		
42	PC	PL	PL	NI	NI	NI	NI		
18	PC	PL	PL	PL	PL	NI	PL		
31	PC	PL	PL	NI	NI	NI	PL		
15	NI	NI	NI	NI	PL	NI	PL		
8	PL	NI	NI	PL	NI	Ni	NI		
10	PL	NI	NI	PL	NI	NI	PL		
25	NI	NI	NI	NI	NI	NI	NI		
41	NI	NI	NI	NI	NI	NI	NI		
20	PL	NI	NI	PL	NI	NI	NI		
23	PL	PL	PL	PL	NI	NI	PL		
29	PL	NI	NI	PL	NI	NI	PL		
14	NI	NI	NI	NI	NI	NI	NI		
36	PL	NI	PL	PL	PL	NI	PL		
44	NI	NI	NI	NI	NI	NI	PL		
43	PL	NI	NI	NI	NI	NI	NI		
				NI	Not inundated				
				PL	PL Partial water (liberal)				
	PC Partial water (conservative)								

Table 3.4: DSWE-predicted wet and dry values for ponds at Alapaha in 2017.

Pond ID	20170115	20170131	20170216	20170304	20170320	20170421	20170507	20170616	mns
46	1	1	1	1	1	1	1	1	8
P5	1	1	1	1	1	1	1	1	8
P1	0	1	1	1	1	1	1	0	6
P4	0	1	1	1	1	0	1	1	6
P6	1	1	1	1	1	0	0	0	5
30	1	1	1	1	1	0	0	0	5
28	0	1	1	1	1	0	0	0	4
P7	0	0	1	0	1	0	0	1	3
3	0	1	0	1	1	0	0	0	3
31	1	1	0	0	0	0	0	0	2
4	0	1	0	1	0	0	0	0	2
18	0	1	0	0	0	0	0	0	1
2	1	0	0	0	0	0	0	0	1
P3	0	0	0	0	0	0	0	0	0
P2	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0

Pond ID	20170115	20170131	20170216	20170304	20170320	20170421	20170507	20170616	wns
25	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0
11	NA	NA							

Table 3.5: Confusion matrix for observed and predicted values of surface water presence in 24 ponds at Alapaha River WMA. The number of ponds recorded as wet and the number of ponds recorded as dry were compared for each paired data set which included 7 survey dates and 7 DSWE scenes.

	actual wet	actual dry
predicted wet	19	0
predicted dry	38	111

Table 3.6: DSWE-predicted wet and dry values for ponds at Alapaha in 2015.

Pond ID	20150110	20150203	20150307	20150331	20150408	20150502	20150518	20150603	20150619	ums
P1	1	1	1	1	1	1	1	1	1	9
P4	1	1	1	1	1	1	1	1	1	9
P5	1	1	1	1	1	1	1	1	1	9
3	1	1	1	1	1	1	0	1	1	8
46	1	1	1	1	1	1	0	0	0	6
8	0	1	1	1	1	0	1	0	1	6
20	0	1	1	1	1	1	0	0	1	6
10	0	1	1	1	1	1	1	0	0	6
P6	1	1	0	1	1	1	0	0	0	5
15	1	1	1	1	1	0	0	0	0	5
28	1	0	1	1	1	1	0	0	0	5
4	1	1	1	1	0	1	0	0	0	5
30	1	1	1	1	1	0	0	0	0	5
P7	1	1	1	1	0	0	0	0	0	4
24	0	0	0	1	1	1	1	0	0	4
39	0	1	1	1	1	0	0	0	0	4
43	0	1	1	1	0	0	1	0	0	4
23	0	1	1	1	0	0	0	0	0	3
18	0	1	1	1	0	0	0	0	0	3
31	1	1	1	0	0	0	0	0	0	3
42	0	1	1	0	0	0	0	0	0	2
32	0	1	1	0	0	0	0	0	0	2
2	0	1	0	0	0	0	0	1	0	2
40	0	1	1	0	0	0	0	0	0	2
P2	0	0	0	1	0	0	0	0	0	1
45	0	0	0	1	0	0	0	0	0	1
22	0	0	0	0	0	0	0	0	1	1
41	0	0	1	0	0	0	0	0	0	1
25	0	0	0	0	0	0	1	0	0	1
26	0	0	0	0	0	0	1	0	0	1
27	0	0	0	0	0	0	0	1	0	1
17	0	0	1	0	0	0	0	0	0	1
14	0	0	1	0	0	0	0	0	0	1
P3	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0

Pond ID	20150110	20150203	20150307	20150331	20150408	20150502	20150518	20150603	20150619	wns
38	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0
11	NA	NA								

Table 3.7: DSWE-predicted wet and dry values for ponds at Alapaha in 2016.

Pond ID	20160113	20160129	20160214	20160301	20160418	20160504	20160621	sum
P4	1	1	1	1	1	1	1	7
P5	1	1	1	1	1	1	1	7
46	1	1	1	1	1	0	0	5
P1	1	0	0	1	1	0	1	4
P6	1	1	1	1	0	0	0	4
3	0	0	0	1	1	1	1	4
P7	0	1	1	1	0	0	0	3
4	0	0	0	1	1	1	0	3
30	0	0	1	1	1	0	0	3
24	0	0	0	1	1	0	0	2
39	0	0	0	1	1	0	0	2
20	0	0	0	0	1	1	0	2
28	0	0	0	1	1	0	0	2
43	0	0	0	0	1	1	0	2
31	0	0	1	1	0	0	0	2
42	0	0	0	1	0	0	0	1
8	0	0	0	0	1	0	0	1
22	0	0	0	0	0	0	1	1
18	0	0	0	1	0	0	0	1
15	0	0	0	0	1	0	0	1
10	0	0	0	0	1	0	0	1
17	0	0	0	0	1	0	0	1
P3	0	0	0	0	0	0	0	0
P2	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0

Pond ID	20160113	20160129	20160214	20160301	20160418	20160504	20160621	sum
25	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0
11	NA	NA						

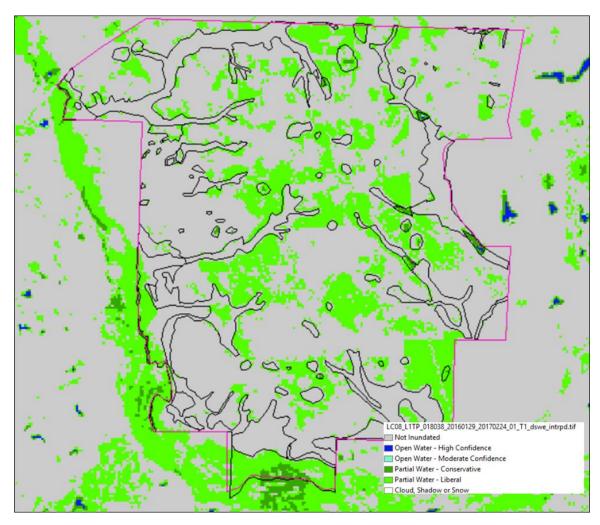


Figure 3.1: An example of a DSWE scene from 29 January 2016 and its classification of pixels across the Alapaha River Wildlife Management Area.

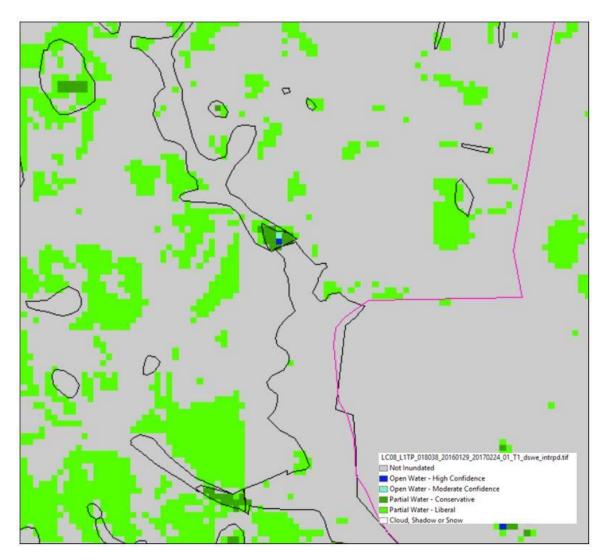


Figure 3.2: A zoomed in view to show values which can be represented by the DSWE interpreted layer.



Figure 3.3: Number of ARWMA study wetlands with water observed and DSWE predicted surface water presence between January and June 2017.

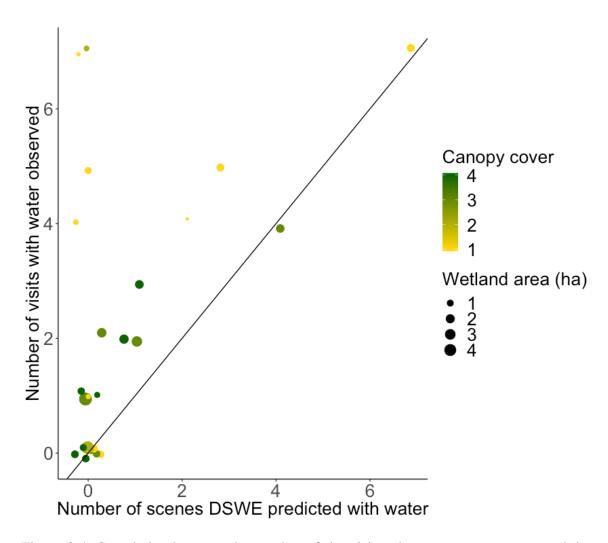


Figure 3.4: Correlation between the number of site visits when water was present and the number of DSWE scenes with predicted water among 24 ARWMA wetlands as a function of wetland area and canopy cover.

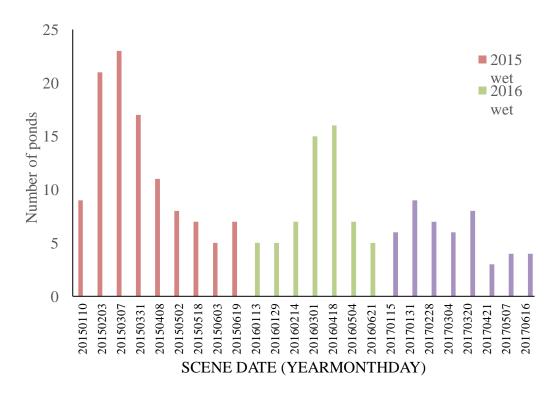


Figure 3.5: The number of ARWMA ponds estimated to have surface water between January and June in 2015, 2016, and 2017. Dates are presented as YEARMONTHDAY.

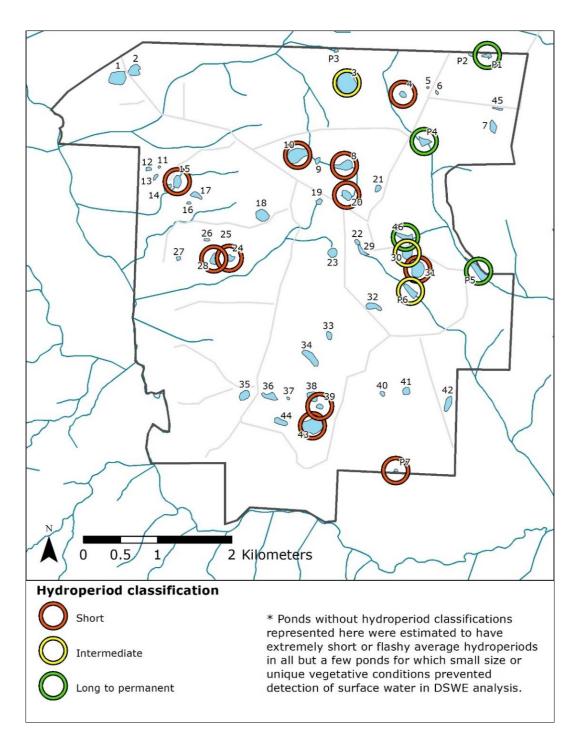


Figure 3.6: Map showing hydroperiod classifications for ARWMA ponds based on DSWE analysis from 2015-2017. Short = 2-3 mean number of scenes per year with water, Intermediate = 4-5 mean number of scenes per year with water, Long to permanent > 5 mean number of scenes per year with water each year.

CHAPTER 4

DEVELOPMENT OF A HABITAT SUITABILITY MODEL TO GUIDE GOPHER FROG MANAGEMENT IN GEORGIA

Introduction

The efficient and effective management of threatened and endangered species requires knowing where taxa occur, identifying areas of suitable or restorable habitat, and choosing actions that are likely to improve persistence among managed populations. All of these elements of effective conservation require information that is not readily available or is costly to generate when needed. This problem is particularly acute for rare or cryptic species that are challenging to detect and often distributed among isolated sites within fragmented landscapes (McGarigal & Cushman, 2002; Knapp, Matthews, Preisler, & Jellison, 2003; Lion, Garda, & Fonseca, 2014). As a result, predictive models are critical to guide decisions. In particular, habitat suitability models are often developed to make predictions about the likelihood that conditions at a particular location would support a particular species.

Within a species' range, the probability that a species occurs in a distinct location is influenced by local processes which are often associated with attributes such as climate, productivity and resource availability, structure and the availability of cover, or refugia, competitors, and predators (Van Buskirk, 2005; Scherer, Muths, & Noon, 2012). Productivity and resource availability, structure, and microclimates are often directly or indirectly related to vegetation and disturbance regimes. In addition, the composition of

land cover and connectivity between habitat patches drive landscape population processes through effects on emigration and immigration. Species occurrence data can be compiled and analyzed to identify relationships and patterns which can inform our understanding of the biological requirements of individual species. Recognizing the patterns that define habitat associations for wildlife species can help us make predictions about their distributions, identify areas most likely to support their populations, and restore natural communities where they are found to promote their persistence on the landscape. The configuration of these land cover features can determine how accessible essential habitats are to wildlife populations.

For species with complex life cycles that require multiple distinct habitats, the development of habitat suitability models can be particularly challenging. Complex life cycles involve dramatic physical transformations coupled with transitions to new habitats (Wilbur, 1984; Werner, 1986, 1988; Moran, 1994). For species with complex life cycles, each life stage reflects a relatively discrete suite of traits adapted for growth or survival in distinct, "complementary" habitats that are required for an animal to complete all phases of its life. Pond-breeding amphibians are well-known examples of species with complex life cycles that require multiple distinct habitats for breeding, terrestrial growth and refuge, aestivation, and overwintering. Therefore, habitat suitability models for amphibians need to consider the availability and configuration of attributes of water bodies, surrounding uplands, and wider landscapes that affect processes such as annual migrations and dispersal (Quesnelle, Fahrig, & Lindsay, 2013; Pittman, Osbourn, & Semlitsch, 2014; Sinsch, 2014; Becker, Fonseca, Haddad, Batista, & Prado, 2007; Cannatella, 2008; Becker, Fonseca, Haddad, & Paulo, 2010). In addition, models must

use variables with sufficiently fine resolution not only to inform management over large landscapes, but to guide local management activities at smaller scales.

Gopher frogs (*Rana capito*) are an example of an aquatic-breeding amphibian with distinct complementary habitat requirements and are a high priority species for management. In the uplands, Gopher frogs are associated with open canopied pine forests with an understory composed of wiregrass and a high diversity of other herbaceous plant species (Franz, 1986; Hammerson & Jensen, 2004). Within the wetlands, these same attributes of vegetative structure appear to be important. Reduced canopy cover over a wetland allows for more light to penetrate through the water and stimulate plant and algal growth, an important nutrient source for larvae (Skelly, Freidenburg, & Kiesecker, 2002; Skelly, Halverson, Freidenburg, & Urban, 2005). Herbaceous emergent plants provide attachment sites for Gopher frogs' clutches as well as cover for the developing larvae, which are reportedly poorer swimmers that spend much more time in hiding than their leopard frog counterparts (J. Jensen GA DNR pers. communication; Gregoire & Gunzburger, 2008).

Gopher frogs breed in isolated wetlands (i.e., wetlands not connected by surface waters to other water bodies) that typically have open canopies and emergent herbaceous vegetation and intermediate hydroperiods. Ponds which are not connected to water sources are less likely to support fish and other important predators of Gopher frogs.

Juvenile and adult Gopher frogs are known to disperse up to ~4 km from breeding wetlands where they occupy tortoise burrows, mammal burrows, and stump holes (Franz, Dodd, & Cheri, 1988; Roznik, Johnson, Greenberg, & Tanner, 2009; Humphries & Sisson, 2012). Half the Gopher frog population may reside in uplands over a half a

kilometer from a breeding site, and 10% of the population may reside over 1 km from a breeding site (J. Maerz and B. Crawford, unpublished data). Gopher frog populations throughout much of their range are distributed among isolated, remnant sites interspersed by extensive areas of unsuitable modified landscapes (Thurgate & Pechmann, 2007; Humphries & Sisson, 2012). As a result, the identification and management of remnant Gopher frog populations and the identification of potentially suitable habitats for reintroductions are a high conservation priority.

In 2003, the GA-GAP land cover dataset and habitat models were developed to map the distribution of habitat for over 400 vertebrate species, including Gopher frogs, throughout Georgia using species-habitat relationships derived from known ranges, occurrence records, and expert input (Kramer et al., 2003). The GAP model for Gopher frogs was developed using the GAP model for Gopher tortoises and then adding a buffer to include nearby wetlands (Kramer et al., 2003). The imagery used to develop the land cover classes for the GAP project is now over two decades old, and the Gopher frog habitat model may not best reflect species-habitat relationships, some of which may only be discerned at finer resolutions.

The objective of this study was to develop a new habitat suitability model for Gopher frogs that included local and landscape predictors for Gopher frog presence, with consideration for the species' biphasic life history. It is generally accepted that Gopher frog population declines are attributable to habitat loss and fragmentation, specifically, conversion of longleaf pine ecosystems to intensive agriculture and plantation forestry and the loss or degradation of the wetlands embedded within these systems. In addition, shifts in upland conditions that reduce the availability of tortoise burrows or other refugia

likely contribute to declining population persistence. By developing and comparing models that integrate wetland and upland variables at local and landscape scales of wetlands where Gopher frogs are known to persist throughout Georgia, I aim to identify the most robust predictors of Gopher frog habitat suitability. I then project that model onto Alapaha River Wildlife Management Area (Chapter 1), where I completed amphibian occupancy studies in Chapter 2 and evaluated wetland hydroperiods in Chapter 3, to assist managers in evaluating current wetland suitability and specific management actions that could improve available Gopher frog habitat and population persistence on the site.

Methods

Study area

The Gopher frog's distribution in Georgia spans numerous ecoregions within the Southeastern Plains and the Coastal Plain. Georgia's coastal plain is characterized by its sandy soils, relatively flat landscapes with low relief, and languid rivers that feed into swamps in low lying areas with poorly draining soils. Freshwater, brackish, and salt marshes intersect the lowest lying areas along the coast; more inland and isolated freshwater wetlands of various origins occur in upland areas throughout the state, with the underlying sediment ranging from clay, to sand, to limestone (Kramer et al., 2003). Current land use in the coastal plain is dominated by row crop agriculture and intensively managed pine forests, with cotton, peanuts, and timber among the top valued commodities of the state (U.S. Department of Agriculture, 2016; The University of Georgia Center for Agribusiness and Economic Development, 2018). In Georgia, Gopher

frogs are often found in conjunction with the Gopher tortoises, which prefer the dry sandy soils and relatively open canopies with herbaceous understories characteristic of natural pine savannas or turkey oak habitats and create burrows that serve as refugia for Gopher frogs. Therefore, Gopher frogs are most closely associated with remnant or restored patches of pine savanna, though they may also be found in more mesic terrestrial habitats than one would expect to find Gopher tortoises (Godley, 1992; Stevenson, Cash, & Jensen, 2007).

Modeling approach

I used known occurrence data for wetlands where Gopher frogs are currently known to persist in Georgia to develop a logistic model of habitat suitability. Generalized linear modeling is a widespread method for habitat suitability modeling, often selected for its flexibility, including link functions that allow the model to accommodate variables with different distributions (i.e., Gaussian and binomial) (A. Guisan, Edwards Jr, & Hastie, 2002). I used generalized logistic models, which require presence and absence or pseudoabsence data (Steven et al., 2009; Jorge, Alberto, & Joaquín, 2010). Selection of known Gopher frog wetlands – The locations for Gopher frog presences were compiled by Georgia Department of Natural Resources Wildlife Resources Division biologists and included locations for each site where eggs, tadpoles, or frogs were found and reported in Georgia since 1932. Of the total 332 records, only seven records were prior to 1960, while 239 were recorded between 2000 and 2018. I only used sites with records since 2000 in constructing my models. Records were organized by detection method and then filtered to exclude records of "burrow" detections, which referred to frogs found in Gopher tortoise burrows, as the breeding site for many of these animals

was unknown. Because I wanted to include attributes of breeding sites in the models, I limited my analysis to records of detections at breeding ponds where Gopher frogs were detected by dipnetting or egg mass surveys. In the DNR data set, all site records for Gopher frogs calling at wetlands were also accompanied by records with visual detections of eggs or larvae. These locations were compared to the locations of wetlands recorded in the National Wetland Inventory (NWI) (U.S. Fish and Wildlife Service, 2018), as well as wetlands in the National Hydrography Dataset (NHD Plus) (U.S. Geological Survey, 2018). When points did not fall within 50 meters of an NWI or NHD wetland, high-resolution 6-inch statewide imagery was reviewed to confirm the presence of a wetland and then I manually delineated the wetland in ArcMap. Selection of pseudoabsence wetlands – I used a method of spatially constrained point selection to generate pseudoabsence points corresponding to unique wetlands (Senay, Worner, & Ikeda, 2013). Pseudoabsence wetlands were constrained to selected areas within Georgia's coastal plain (Zarnetske, Thomas C. Edwards, & Moisen, 2007) and represented a subset of wetland types known to support Gopher frog populations. Polygons were drawn to represent the boundaries of several individual, well-surveyed WMAs and properties throughout South Georgia where all ponds used by Gopher frogs were likely to have been documented (J. Jensen Georgia Department of Natural Resources, pers. comm.), as well as several areas identified by DNR biologists as sites where they did not believe Gopher frogs currently occurred (J. Maerz and B. Crawford, unpublished work; J. Jensen Georgia Department of Natural Resources, pers. comm.). Points were generated from within these polygons, but only when they corresponded to freshwater emergent wetlands, freshwater ponds, forested/shrub wetlands, and small

lakes included in the National Wetland Inventory (NWI) (Hammerson & Jensen, 2004). To avoid comparisons between known Gopher frog wetlands and clearly unsuitable wetland habitats, I excluded riverine wetlands as well as forested/shrub wetlands and lakes with areas exceeding 80 hectares. Forested wetlands are the most abundant wetlands occurring on this landscape, but they are overrepresented in the NWI due to the classification methods used for riverine wetlands and extensive floodplain swamps. For example, random generation of 300 points within wetlands from targeted areas throughout the Gopher frog's range resulted in the exclusion of all but forested/shrub wetland types. To ensure that I could collect a representative sample of wetland types available, I generated 5,000 random points within wetlands from the refined NWI layer and within the polygons described above; I then manually selected wetlands from this larger set of points, spatially distributing 103 selections across the polygons while avoiding selection of multiple wetlands from the same riverine/floodplain complex. A sufficient number of wetlands was selected to allow for an approximately 2:1 ratio between pseudoabsence wetlands and presence wetlands (Liu, Newell, & White, 2016). I used these targeted background points, rather than random points, to train my model to distinguish between suitable and highly suitable habitats. When true absence data are lacking, the careful selection of background points, using biological knowledge, is recommended to improve the predictive power of habitat suitability models (Zarnetske et al., 2007; Jorge et al., 2010; Antoine Guisan, Thuiller, & Zimmermann, 2017). Selections of pseudoabsence wetlands were compared with presence wetlands to ensure that no wetland was included in both sets.

Landscape analysis and generation of predictor variables — Wetland and upland attributes were extracted from both sets of wetlands, with some attributes collected at multiple spatial scales: the pond basin, a 100 m buffer around each pond, and a 1 km buffer around each pond (Table 4.1). The 100 m buffer was chosen to represent the ecotone or the "natal patch" which would be experienced by juvenile metamorphs as they emigrate from the natal pond into upland habitat, and by adults during breeding migrations (Sinsch, 2014). The 1 km buffer represents the surrounding terrestrial habitats which would be available to most Gopher frogs, given their average movements/home range sizes as reported in the literature for Gopher frogs (Franz et al., 1988; Blihovde, 2006; E. A. Roznik & Johnson, 2009a; Humphries & Sisson, 2012). An ongoing study of Gopher frog detections at burrows and wetland sites throughout their reported range suggests that 90% of individuals and their terrestrial refuges would be included within a 1 km buffer from the pond (J. Maerz and B. Crawford, unpublished data).

Predictor variables represented characteristics of hydrology, land cover, forest structure, and soil, which may influence habitat use by Gopher frogs. Land cover data were obtained from the 2011 National Land Cover Database (NLCD), derived from Landsat imagery with 30m pixel resolution (Homer et al., 2015). To identify important land cover relationships, I included the percentage land cover for fourteen NLCD classes within a pond, the 100 m buffer including the pond, and the 1 km buffer including the pond. Evergreen and Mixed Forest land cover classes were merged to represent both pine and pine-oak forests, and Low and Medium Intensity Developed Areas were merged as well (Table 4.1). Percentage land cover was calculated for these and the following classes: Open Water, Developed Open Space, Barren Land, Deciduous Forest,

Grassland/Herbaceous, Pasture/Hay, Cultivated Crops, Woody Wetlands, and Emergent Wetlands. I also had access to a forest structure data set which includes percentage of dominant cover by forbs, by shrubs, and by tree canopy, also derived from Landsat imagery, but which used multi-season imagery to map forest structural attributes in each 30m pixel (T. Prebyl, personal communication).

Hydrologic isolation of each study pond was estimated by assessing each pond's connection to other waters, including any streams, ditches, and/or permanent water, in ArcGIS (Version 10.6.1). Any ponds which were within five meters of the National Hydrography Database (NHD) flowline were considered to have structural hydrologic connectivity (Bracken et al., 2013; Golden et al., 2017). These ponds were categorized as connected (1); ponds which were not situated within five meters of an NHD flowline were categorized as isolated (0) (Table 4.1). The NHD flowline represents both streams and artifical connections including ditches, a common occurrence in silvicultural sites.

I calculated the number of nearby (within 100 m and 1 km) wetlands in ArcGIS to investigate the effects of distance between wetlands on the landscape as they relate to Gopher frog occurrence (Table 4.1).

Because Gopher frogs rely on underground retreats and are commonly associated with Gopher tortoise burrows, I included soil suitability for Gopher tortoises from the as a predictor variable (NRCS, 2017; Table 4.1).

Habitat suitability model development – For both Gopher frog wetlands and pseudoabsence wetlands, I created buffers of 100 m and 1 km in ArcGIS to represent a local and landscape scale context for each wetland. I converted the wetland vector layers to raster for the Gopher frog wetlands and the pseudoabsence wetlands and used the

Focal Statistics tool to calculate wetland area in hectares. I did the same for both the 100 m and 1 km buffers. I then calculated the percentage land cover for each of my eleven classes (including two classes representing the merged classes of Evergreen with Mixed Forest and Developed Low with Developed Medium Intensity) at each of the three scales. I calculated the percentage of Gopher tortoise suitable soils for only the 100 m and 1 km buffers surrounding wetlands. I constructed a Pearson's r correlation matrix to identify covariates which were highly correlated (defined as less than -0.6 or greater than 0.6). I used the *dredge* function in package MuMin to generate a set of logistic regression models using combinations of the terms in the global model to predict Gopher frog presence or absence (Barton 2018; R Development Core Team, 2018). The dredge function could accommodate up to 30 predictor variables in a GLM framework, so I included all variables unless they were highly correlated or were unlikely to occur and/or influence habitat relationships (i.e., Developed Low and Medium Intensity within the wetland). The *dredge* function also allows one to include rules for inclusion, so I used to it run one GLM with up to five independent variables and one univariate model to identify parameters with the strongest influence on Gopher frog presence. The glm function uses a logit link to accommodate the binary output of the response variable, which is presence (1) or absence (0) of Gopher frogs, and the binary response variable depends on a set of explanatory variables.

From the dredged output for univariate models best predicting Gopher frog occurrence, I selected the top nine variables which were not highly correlated. I included these variables in a set of candidate models along with the predictor variable, connected, which related to the ponds' hydrological connections to other ponds, and Gopher tortoise

soil suitability at the 100 m and 1 km scales. From this set of variables, I then developed candidate models based on known relationships about how local and landscape-level variables influence Gopher frog presence (Table 4.2). I limited my candidate models to include combinations of up to five independent variables to avoid overparameterization. All analyses were conducted in R and ArcGIS (R Development Core Team, 2018). *Model projection into the Alapaha River Wildlife Management Area*

The top performing model then was used to predict the suitability of 53 ponds for Gopher frogs within the Alapaha River Wildlife Management Area (ARWMA). The same variables collected for the known Gopher frog and pseudoabsence wetlands were collected for each ARWMA pond and its two buffers as appropriate (Chapter 2, Figure 2.1) The *predict* function in R was used to estimate Gopher frog habitat suitability for each pond. I divided the possible range of suitability into four ranges: < 0.75; 0.75–0.85; 0.85–0.95; and 0.95–1.0 (R Development Core Team, 2018).

Hydroperiod assessment for highly suitable and moderately suitable ponds at ARWMA

An overlay of estimates for classification of hydroperiod (see Chapter 3, Figure 3.6) was used to further evaluate pond sites which the habitat suitability model identified as moderately or highly suitable. The habitat suitability model did not include any measures of hydroperiod due to the limited geographical extent of my hydroperiod analysis described in Chapter 3. For that analysis, I had identified ARWMA ponds with the longest average hydroperiods from 2015–2017. Results from that analysis were overlaid with the habitat suitability estimates to further refine the habitat model results.

Results

Of the 332 Gopher frog detections provided by DNR, 42 locations in 11 counties represented ponds where Gopher frogs had been detected post-2000 (Baker, Bryan, Camden, Chattahoochee, Emanuel, Evans, Long, Liberty, Tatnall, Taylor, and Marion counties). A wetland complex associated with an introduced Gopher frog population but with no historic record of occurrence in Early County was excluded from the analysis. The presence wetland data set included 19 forested/shrub wetlands (0.36—14.56 ha in size), 10 freshwater ponds (0.24—3.72 ha), 13 freshwater open canopy wetlands with emergent vegetation (0.12—7.32 ha), and 2 riverine wetlands (0.04 and 0.72 ha).

The pseudoabsence data set included a total of 103 wetlands and included 92 forested/shrub wetlands (0.16—92.47 ha in size), 4 freshwater ponds (1.53—8.57 ha), 5 freshwater emergent wetlands (0.74—616.57 ha), and 2 small freshwater lakes (8.21 and 9.87 ha).

A connection to streams, ditches, or permanent water was identified in only 14 % of the Gopher frog ponds, compared with 22 % of pseudoabsence wetlands (Table 4.1). The mean number of wetlands within 100 m was 1 (SD = 1) versus 4 (SD = 3) and within 1 km was 18 (SD = 9) versus 32 (SD = 20) for Gopher frog versus pseudoabsence wetlands respectively.

Land cover within both the 100 m and 1 km buffer of Gopher frog ponds was dominated by evergreen and mixed forest (44.7 % and 45.7 % respectively) (Table 4.1). Grasslands/herbaceous land cover (class 71) was of relatively equal importance at 100 m and 1 km scales, with the class comprising a mean of 13.9 % of the 100 m buffer and 11.3 % of the 1 km buffer. For pseudoabsence wetlands, woody wetlands comprised the

largest proportion of the 100 m buffer (46.5 %) and the 1 km buffer (36.7 %), whereas Gopher frog wetland buffers contained evergreen and mixed forest. Gopher frog pond buffers. Grasslands/herbaceous land cover (nlcd71) was much more scarce surrounding pseudoabsence wetlands, with the class comprising only 4.7 % of the 100 m buffer and 5.9 % of the 1 km buffer. Within the 100 m buffer, 36 % of the buffer contained suitable Gopher tortoise soils, increasing to 43 % within the 1 km buffer; double the amount surrounding pseudoabsence wetlands (17 % at 100 m buffer and 24 % at 1 km buffer).

Total canopy cover was relatively low for Gopher frog ponds, with the lowest cover corresponding to the wetland basin (17.8 %) and the highest cover estimated at the 1 km scale (21.6 %) (Table 4.1). Forbs and grass cover were greatest within the wetland (39.3 %) but remained the dominant understory at the 100 m (34.7 %) and 1 km (29.4 %) scales. Pseudoabsence wetlands exhibited an inverse relationship, with total canopy cover highest within the pond (37.4 %) and forbs and grass cover lowest within the pond (18.8 %). Shrub cover was more similar between the two sets of ponds, but it was consistently higher at each scale for pseudoabsence wetlands.

Habitat suitability models

The univariate model which best predicted Gopher frog presence included forbs/grass within the wetland (Figure 4.1). The top ranked global models also included forbs/grass within the wetland, evergreen and mixed forest at 100 m and 1 km, and number of wetlands within 100 m and within 1 km. The top performing multivariate models (4) included four variables: forbs and grasses, Gopher tortoise suitable soils, evergreen and mixed forest, and number of nearby wetlands, and with all three scales represented (Table 4.3). According to this model, the probability of Gopher frog presence was positively

correlated with the percentage of forb and grass cover within the wetland basin, the percentage of Gopher tortoise suitable soils within 100 meters of the wetland, and the percentage of evergreen and mixed forest within 1 km of the wetland. Gopher frog presence was slightly negatively correlated with the number of other wetlands within 100 m. The next best performing model was within 2 AIC of my top model and had the same four predictor variables plus an additional predictor variable of the percentage of grasslands/herbaceous land cover within 100 m. While Gopher frog presence and pseudoabsence wetlands both spanned nearly the full range of predicted probability of Gopher frog presence [suitability], the distributions of probability scores for wetlands was highly divergent and showed little overlap (Figure 4.2).

Model projection over Alapaha River Wildlife Management Area

I used my top model (Table 4.3, #4) to estimate suitability for the Gopher frog at 52 of 53 discrete wetlands at Alapaha. The small size of one pond (Pond 37; 0.07 ha) precluded me from collecting covariates for its inclusion in the habitat suitability analysis. The model estimated the suitability of individual ponds as ranging from 0.026 to 0.996, with the mean for all sites estimated at 0.795. Standard errors for these estimates ranged from 0.004 to 0.259, with the mean standard error for all predictions estimated at 0.084. Seventeen ponds were estimated to have >0.95 suitability for Gopher frogs (Appendix 4.1, Figure 4.3).

Ponds with suitability exceeding 0.99 include 3, 4, 15, 32, 5, and 27 (Appendix 4.1, Figure 4.3). Pond 3 is the pond where Gopher frogs were detected on the property (Chapter 2). Pond 4 is a 0.34-ha herbaceous emergent pond located to the east of pond 3 and within the same power line clearing, but closer to a creek. Pond 15 is a 1.29-ha

cypress-gum pond with \sim 75 % canopy cover and located on the northwestern side of the property. Pond 32 was not one of my prior study ponds, but it was visited on two occasions and estimated to have less than 50% canopy cover. Ponds 5 and 27 are less than 0.2 ha in size and were not visited during the course of the study. Forest structure estimates for both ponds are similar to those for ponds where canopy cover was estimated to be between 25–50 % (covmax = 20.77 % for pond 5 and 28.0 % for pond 27; forbgrass = 36.1 % for pond 5 and 29.61 % for pond 27).

Ponds with suitability of 0.98–0.99 include ponds 25, P4, 8, 10, and P6 (Appendix 4.1, Figure 4.3). Pond 25 is an open canopy ~0.52 ha pond with emergent herbaceous cover and a shallow basin. P4 and P6 represent artificial impoundments. Ponds 8 (~2.24 ha) and 10 (~4.82 ha), on the northern end of the property, are both mixed herbaceousforested ponds with canopy cover exceeding 50%.

Hydroperiod considerations for ponds with highest estimated suitability

An overlay of estimates for classification of hydroperiod was used to further evaluate ponds which the habitat suitability model identified as moderately or highly suitable. Ponds with the longest reported hydroperiods were typically permanently wet. Ponds with green, yellow, and red rings (Figure 4.4) represent the ponds that the DSWE analysis identified as having an average of at least two consecutive scenes of surface water each year between January and July for three years (2015–2017). Hydroperiod classifications were determined by the mean annual number of scenes for which surface water was detected (see Chapter 3). Of the seventeen ponds that the habitat suitability model identified as highly suitable, only four had intermediate or long hydroperiods. Of

these four, ponds 3 and P6 were classified as having intermediate hydroperiods, and pond 46 and P4 were classified as long-to-permanent.

Discussion

I was able to evaluate habitat suitability models that considered wetland and upland attributes at various scales to predict the likelihood of Gopher frog presence in Georgia. Importantly, variables at all three scales (the pond basin, 100 m, and 1 km) were all represented in the top model and included both wetland and terrestrial habitat variables of known importance to different life stages of Gopher frogs. The presence of forbs or grasses within the pond basin was a strong predictor for Gopher frog presence. The cover of forbs or grasses may be indicative of wetlands with intermediate to long hydroperiods. Periods of intermittent draw down would allow for grasses and facultative and obligate wetland plants to establish and for periodic fires to pass through wetland margins or basins, which can reduce the encroachment of shrubs and trees (Thurgate & Pechmann, 2007; Freeman & Jose, 2009). Additionally, these wetlands with grasses and forbs present may be reflecting a history of growing season fires that are able to move through wetlands when they are dry. Fire can burn through organic woody matter, deepening the wetland basin and promoting structural heterogeneity in vegetation (Kirkman, 1993; Kirkman & Sharitz, 1994; Mitchell et al., 1999). The presence of grasses may also indicate high wetland productivity to support Gopher frog larval development. Variation in larval growth rate is primarily related to resource availability (Rose, 2005; Wells, 2007), and variation in canopy openness and associated allochthonous plant resources is an important gradient determining larval performance

(Skelly et al., 2002; Rubbo & Kiesecker, 2004; Maerz, Brown, Chapin, & Blossey, 2005; Brown, Blossey, Maerz, & Joule, 2006; Rubbo, Belden, & Kiesecker, 2008; Williams, Rittenhouse, & Semlitsch, 2008; Earl, Luhring, Williams, & Semlitsch, 2011; Rittenhouse, 2011; Stoler & Relyea, 2011; Adams & Saenz, 2012; Cohen, Maerz, & Blossey, 2012; Cotten, Kwiatkowski, Saenz, & Collyer, 2012; Earl, Cohagen, & Semlitsch, 2012; Stephens, Berven, & Tiegs, 2013; Martin, Rainford, & Blossey, 2014). Plant detritus varies in nutrient and secondary compound concentrations. Most tree species litter is low in nutrients or has high concentrations of secondary compounds that limit productivity (Earl et al., 2012). In contrast, herbaceous plants such as grasses and sedges are richer in nitrogen and phosphorus and have lower concentrations of secondary metabolites. In combination with high light, herbaceous plants support higher primary production, shorter amphibian larval periods, and larger sizes at metamorphosis (Williams, Rittenhouse, & Semlitsch, 2008; Maerz et al., 2010; Cohen, et al., 2012; Earl & Semlitsch, 2013).

Evergreen and mixed forest land cover and Gopher tortoise soil suitability at broader scales were also important predictors of Gopher frog presence. Gopher tortoise soil suitability was most important within 100 meters of ponds. These results are similar to an analysis of land cover surrounding Gopher frog ponds in Florida that identified sandhills as the most common land cover within 300 meters of Gopher frog ponds (Enge et al., 2014). Multiple telemetry studies following juvenile and adult Gopher frogs have found that many of the frogs, while capable of making long-distance movements, select refuges, often tortoise burrows, within 250 meters of their pond (Phillips, 1995; Blihovde, 2006; E. A. Roznik & Johnson, 2009b), and a recent analysis of Gopher frog occurrences

within tortoise burrows found that 50% of Gopher frogs within tortoise burrows are within 400 m of the nearest wetland (J. Maerz and B. Crawford, unpublished data). At the 1 km scale, evergreen and mixed forest was indicative of the more open pine savanna and turkey oak habitats associated with Gopher frogs and Gopher tortoises.

I had anticipated that the top model would include proximity to other wetlands as a strong predictor for Gopher frog presence. Generally, proximity to other wetlands is expected to increase amphibian population persistence because it provides for larger populations, a wider range of hydroperiods to support breeding under variable weather conditions, and opportunities for rescue events from neighboring sites (Semlitsch, 2003; Petranka, Smith, & Scott, 2004). I found only a weak negative relationship between number of nearby wetlands and Gopher frog presence at the 100 m and 1 km scales. It is possible that Gopher frogs' extreme incompatibility with fish results in their survival at only the most isolated (i.e., protected) breeding ponds. It seems more likely that my results were an artefact of the NWI's classification methods for floodplain wetlands and the limited representation of wetlands included in my pseudoabsence wetland data set. High values for number of nearby wetlands, as was measured in this analysis by the number of wetlands within 100 m and 1 km buffers, more appropriately describes the availability of swamp and floodplain wetlands within those buffers than it describes the availability of the geographically isolated wetlands I expected are important for Gopher frogs. Future efforts to model wetland availability and connectivity should seek appropriate methods to more carefully code for the types or classifications of nearby wetlands.

Projected Gopher frog habitat suitability at Alapaha River Wildlife Management Area

The model projections accurately identified the single known Gopher frog pond at ARWMA as having a 0.996 probability of Gopher frog presence; the highest estimate for all ponds on the site (Appendix 4.1, Figure 4.2). This provides reasonable confidence in the utility of the habitat suitability model. However, the model also identified other wetlands as highly or moderately suitable though there is high confidence that Gopher frogs do not currently occupy those sites (Chapter 2). Although it is possible that many sites are suitable but unoccupied due to extremely small population size, it seems more likely that the model is overprojecting the number of currently suitable sites. This apparent overprojection of suitable ponds at ARWMA is likely related to additional factors including hydroperiod and the presence of predators that were not included in the suitability model. Other ARWMA ponds with > = 0.95 predicted probability of Gopher frog presence included one semi-permanent impoundment which supported the highest number of amphibian species found at any single pond in Alapaha in 2016–2017; three permanent impoundments that likely support fish; and a suite of ponds that were connected by a ditch as part of prior efforts to drain those ponds for forestry (see also Chapter 3). Because of these alterations, these ponds have short or flashy hydroperiods (Chapter 3) that are likely too short in most years to support Gopher frog larval development (Chapter 2). This suggests that restoration of the hydroperiod at those additional wetlands by removing the ditch and reducing surrounding forest cover would significantly increase the number of wetlands capable of supporting Gopher frogs at ARWMA. In addition, this demonstrates the need to integrate hydroperiod data into

habitat suitability models for Gopher frogs and other priority amphibians (see also Chapter 3).

The performance of my top model improves upon projections from the prior Georgia GAP model for the Gopher frogs. The GAP model projects a distribution of suitable Gopher frog habitat sweeping across the northwestern side and the southeastern corner of ARWMA while classifying a wide swath of xeric to mesic flatwoods and uplands as unsuitable habitat (Figure 4.5). While the GAP model did capture the one pond (Pond 3) occupied by Gopher frogs, this site occurs on the periphery of the GAP projected suitable habitat. The large areas classified as unsuitable by the GAP model include the area where my model predicts the highest concentration of most suitable ponds for Gopher frogs (Figure 4.2). When comparing the Georgia GAP distribution with the wetland and vegetation communities map in Figure 2.1 (Chapter 2), the GAP model appears to be predicting areas of bay and creek swamps as unsuitable. My single visual detection of a Gopher frog at Alapaha occurred within one of these creek swamp drainages between ponds 3 and 4, and the Gopher frog which was found in a trap in 2014 was found in the northeast corner, as well, adjacent to a creek swamp drainage. These features, which the more terrestrially focused GAP model excludes, may be important features on the landscape for Gopher frogs as they make dispersal or migration movements. My new model identifies potential suitable Gopher frog habitat at ARWMA by evaluating habitat conditions at scales relevant to the Gopher frog and its complex life cycle, providing more reasonable projections to guide management for Gopher frogs on the site.

Limitations

Some limitations of my study include the inability to include locations where Gopher frogs are only known from detections in Gopher tortoise burrows. Detections in tortoise burrows represent the majority of Gopher frog locations known since 2000, but the breeding wetlands associated with these terrestrial locations are not known. By using only records from known breeding locations, I am assuming that those locations sampled were representative of Gopher frog breeding habitats. It is possible that there is bias in terms of the sites selected for surveying Gopher frog egg masses or tadpoles, in which case my model would reflect that bias. For example, if biologists were more likely to survey for Gopher frog egg masses or tadpoles in wetlands with open canopies and emergent herbaceous vegetation, that would predispose those variables to be present in top models. An alternative option would have been to assign the nearest known wetland to all Gopher frog records where the breeding site is not known and assume that wetland was the likely breeding site. However, given the extensive distances Gopher frogs are known to travel between terrestrial burrows and breeding sites, there is a reasonable probability that non-breeding wetlands would have been included as known sites in the analysis, introducing uncertainty into the models that would obscure wetland characteristics important to predicting the presence of Gopher frog breeding.

Because private properties were more likely to not have been surveyed, I did not include wetlands from private properties as candidate sites for pseudoabsences. Instead, I limited my selections to eight polygons, several of which were identified as areas where Georgia Department of Natural Resources biologists did not believe Gopher frogs occurred. As a result, it is likely that I was selecting many pseudoabsence sites from areas

where habitat suitability was low, while reducing the likelihood of selecting pseudoabsence sites from areas with more moderately suitable habitats. This may have created stronger apparent habitat differences between sites with and without Gopher frogs than is representative of actual conditions. Future models may consider alternative approaches to generating pseudoabsences, though all approaches have limitations and tradeoffs (Engler, Guisan, & Rechsteiner, 2004; Steven et al., 2009; Jorge et al., 2010; Barbet-Massin, Jiguet, Albert, & Thuiller, 2012).

Despite continued advances in remote sensing, modeling suitable habitat for species that rely on ephemeral wetlands will continue to be hindered until higher resolution digital resources become more uniformly available to accurately map and classify small wetland features which provide valuable habitat to so many wildlife species.

Literature Cited

- Adams, C. K., & Saenz, D. (2012). Leaf litter of invasive Chinese tallow (Triadica sebifera) negatively affects hatching success of an aquatic breeding anuran, the Southern Leopard Frog (*Lithobates sphenocephalus*). *Canadian Journal of Zoology*, 90(6), 991-998.
- Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, *3*, 327-338.
- Kamil Barton (2018). MuMIn: Multi-Model Inference. R package version 1.42.1. https://CRAN.R-project.org/package=MuMIn
- Becker, C. G., Fonseca, C. R., Haddad, C. F. B., Batista, F., & Prado, P. I. (2007).Habitat Split and the Global Decline of Amphibians. *Science*(5857), 1775.doi:10.1126/science.1149374
- Becker, C. G., Fonseca, C. R., Haddad, C. F. B., & Paulo, I. P. (2010). Habitat Split as a Cause of Local Population Declines of Amphibians with Aquatic Larvae.

 Conservation Biology(1), 287. doi:10.1111/j.1523-1739.2009.01324.x
- Blihovde, W. B. (2006). Terrestrial Movements and Upland Habitat Use of Gopher Frogs in Central Florida. *Southeastern Naturalist*, *5*(2), 265-276.
- Brown, C. J., Blossey, B., Maerz, J. C., & Joule, S. J. (2006). Invasive plant and experimental venue affect tadpole diet and performance. *Biological Invasions*, 8, 327-338.

- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. 2nd Edition, New York: Springer-Verlag.
- Cannatella, D. C. (2008). Comment on "Habitat split and the global decline of amphibians". *Science (New York, N.Y.), 320*(5878), 874; author reply 874. doi:10.1126/science.1155114
- Cohen, J. S., Maerz, J. C., & Blossey, B. (2012). Traits, not origin, explain impacts of plants on larval amphibians. *Ecological Applications*, 22(1), 218-228.
- Cotten, T. B., Kwiatkowski, M. A., Saenz, D., & Collyer, M. (2012). Effects of an invasive plant, Chinese tallow (*Triadica sebifera*), on development and survival of anuran larvae *Journal of Herpetology*, 46, 186-193.
- Earl, J. E., Cohagen, K. E., & Semlitsch, R. D. (2012). Effects of leachate from tree leaves and grass litter on tadpoles. *Environmental Toxicology and Chemistry, in press*.
- Earl, J. E., Luhring, T. M., Williams, B. K., & Semlitsch, R. D. (2011). Biomass export of salamanders and anurans from ponds is affected differentially by changes in canopy cover. *Freshwater Biology*, *56*, 2473-2382.
- Earl, J. E., & Semlitsch, R. D. (2013). Carryover effects in amphibians: Are characteristics of the larval habitat needed to predict juvenile survival? *Ecological Applications*, 23(6), 1429-1142.
- Enge, K. M., Farmer, A. L., Mays, J. D., Castellón, T. D., Hill, E. P., & Moler, P. E. (2014). Survey of winter-breeding amphibian species. Gainesville, FL: Florida

- Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Lovett E. Williams, Jr. Wildlife Research Laboratory.
- Engler, R., Guisan, A., & Rechsteiner, L. (2004). An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data, *Journal of Applied Ecology*. *41*(2), 263-274.
- Franz, R. (1986). Gopherus polyphemus (Gopher tortoise) Burrow commensals. Herpetological Review, 17(3), 64-64.
- Franz, R., Dodd, C. K., & Cheri, J. (1988). Rana areolata aesopus (Florida gopher frog)

 Movement. *Herpetological Review*, 19(4), 82-82.
- Freeman, J. E., & Jose, S. (2009). The role of herbicide in savanna restoration: Effects of shrub reduction treatments on the understory and overstory of a longleaf pine flatwoods. *Forest Ecology and Management*, 257, 978-986. doi:10.1016/j.foreco.2008.10.041
- Godley, J. S. (1992). Threatened: Gopher frog *Rana capito* LeConte. In P. E. Moler (Ed.), *Rare and Endangered Biota of Florida* (Vol. 3: Amphibians and Reptiles, pp. 15-19). Gainesville, FL: Univ. Press of Florida.
- Gregoire, D. R., & Gunzburger, M. S. (2008). Effects of Predatory Fish on Survival and Behavior of Larval Gopher Frogs (*Rana capito*) and Southern Leopard Frogs (*Rana sphenocephala*). *Journal of Herpetology*(1), 97.
- Guisan, A., Edwards Jr, T. C., & Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene, *Ecological Modeling*. 157: 89-100.

- Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat Suitability and Distribution Models With Applications in R*. New York, NY: Cambridge University Press.
- Hammerson, G., & Jensen, J. B. (2004). Lithobates capito. *IUCN 2012. IUCN Red List of Threatened Species*. Retrieved from www.iucnredlist.org
- Homer, C., Dewitz, J., Yang, L., Jin, S., Danielson, P., Xian, G., . . . Megown, K. (2015).
 Highlight Article: Completion of the 2011 National Land Cover Database for the
 Conterminous United States Representing a Decade of Land Cover Change
 Information. *Photogrammetric Engineering & Remote Sensing*, 81, 345-354.
 doi:10.1016/S0099-1112(15)30100-2
- Humphries, W. J., & Sisson, M. A. (2012). Long Distance Migrations, Landscape Use, and Vulnerability to Prescribed Fire of the Gopher Frog (*Lithobates capito*). *Journal of Herpetology*, 46(4), 665-670. doi:10.1670/11-124
- Jorge, M. L., Alberto, J.-V., & Joaquín, H. (2010). The uncertain nature of absences and their importance in species distribution modelling. *Ecography*(1), 103. doi:10.1111/j.1600-0587.2009.06039.x
- Kirkman, L. K. (1993). *Impacts of Fire and Hydrological Regimes on Vegetation in*Depression Wetlands of Southeastern USA. Paper presented at the Tall Timbers

 Fire Ecology Conference, Tallahassee, FL.
- Kirkman, L. K., & Sharitz, R. R. (1994). Vegetation Disturbance and Maintenance of Diversity in Intermittently Flooded Carolina Bays in South Carolina. *Ecological Applications*(1), 177. doi:10.2307/1942127

- Knapp, R. A., Matthews, K. R., Preisler, H. K., & Jellison, R. (2003). Developing Probabilistic Models to Predict Amphibian Site Occupancy in a Patchy Landscape. *Ecological Applications*(4), 1069.
- Kramer, E., Conroy, M. J., Elliot, M. J., Anderson, E. A., Burnback, W. R., & Epstein., J. (2003). *The Georgia Gap Analysis Project Final Report*. Georgia Cooperative Fish and Wildlife Research Unit, Athens, GA.
- Lion, M. B., Garda, A. A., & Fonseca, C. R. (2014). Split distance: a key landscape metric shaping amphibian populations and communities in forest fragments.

 *Diversity and Distributions, 20(11), 1245.
- Liu, C., Newell, G., & White, M. (2016). On the selection of thresholds for predicting species occurrence with presence-only data. *Ecology and Evolution*, *6*, 337-348).
- Maerz, J. C., Brown, C. J., Chapin, C. T., & Blossey, B. (2005). Can secondary plant compounds of an invasive plant affect larval amphibians? *Functional Ecology, 19*, 970-975.
- Maerz, J. C., Cohen, J. S., & Blossey, B. (2010). Does detritus quality predict the effect of native and non-native plants on the performance of larval amphibians?

 Freshwater Biology, 55, 1694-1704.
- Maerz, J. C., Cohen, J. S., & Blossey, B. (2010). Does detritus quality predict the effect of native and non-native plants on the performance of larval amphibians? . *Freshwater Biology*, 55, 1694-1704.
- Martin, L. J., Rainford, S.-k., & Blossey, B. (2014). Effects of plant litter diversity, species, origin and traits on larval toad performance. *Oikos*, n/a-n/a. doi:10.1111/oik.01745

- McGarigal, K., & Cushman, S. A. (2002). Comparative Evaluation of Experimental Approaches to the Study of Habitat Fragmentation Effects. *Ecological Applications*(2), 335.
- Mitchell, R. J., Katherine Kirkman, L., Pecot, S. D., Wilson, C. A., Palik, B. J., & Boring,
 L. R. (1999). Patterns and controls of ecosystem function in longleaf pine wiregrass savannas. I. Aboveground net primary productivity, *Canadian Journal*of Forest Research 29: 743–751
- Moran, N. A. (1994). Adaptation and constraint in the complex life cycles of animals.

 Annual Review of Ecology and Systematics, 25, 573-600.
- NRCS. (2017). *Gopher Tortoise Habitat Suitability Rating* (v6.6). Unpublished report, National Resource Conservation Service.
- Petranka, J. W., Smith, C. K., & Scott, A. F. (2004). Identifying the Minimal Demographic Unit for Monitoring Pond-Breeding Amphibians. *Ecological Applications*(4), 1065.
- Phillips, K. M. (1995). Rana capito capito, The Carolina Gopher Frog, in Southeast

 Georgia: Reproduction, Early Growth, Adult Movement Patterns, and Tadpole

 Fright Response. Unpub. masters thesis. Georgia Southern University. Statesboro.
- Pittman, S. E., Osbourn, M. S., & Semlitsch, R. D. (2014). Perspective: Movement ecology of amphibians: A missing component for understanding population declines. *Biological Conservation*, *169*, 44-53. doi:10.1016/j.biocon.2013.10.020
- Quesnelle, P. E., Fahrig, L., & Lindsay, K. E. (2013). Effects of habitat loss, habitat configuration and matrix composition on declining wetland species. *Biological Conservation*, *160*, 200-208. doi:10.1016/j.biocon.2013.01.020

- R Development Core Team. (2018). Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org
- Rittenhouse, T. A. G. (2011). Anuran larval habitat quality when reed canary grass is present in wetlands. *Journal of Herpetology*, 45(4), 491-496.
- Rose, C. S. (2005). Integrating ecology and developmental biology to explain the timing of frog metamorphosis. *Trends in Ecology and Evolution*, 20(3), 129-135.
- Roznik, E. A., & Johnson, S. A. (2009a). Burrow Use and Survival of Newly

 Metamorphosed Gopher Frogs (*Rana capito*). *Journal of Herpetology*, 43(3), 431437.
- Roznik, E. A., & Johnson, S. A. (2009b). Canopy Closure and Emigration by Juvenile

 Gopher Frogs. *The Journal of Wildlife Management*(2), 260. doi:10.2193/2007-493
- Roznik, E. A., Johnson, S. A., Greenberg, C. H., & Tanner, G. W. (2009). Terrestrial movements and habitat use of gopher frogs in longleaf pine forests: A comparative study of juveniles and adults. *Forest Ecology and Management*, 259(2), 187-194. doi:10.1016/j.foreco.2009.10.007
- Rubbo, M. J., Belden, L. K., & Kiesecker, J. M. (2008). Differential responses of aquatic consumers to variations in leaf-litter inputs. *Hydrobiologia*, 605, 37-44.
- Rubbo, M. J., & Kiesecker, J. M. (2004). Leaf litter composition and community structure: translating regional species changes into local dynamics. *Ecology*, 85(9), 2519-2525.

- Scherer, R. D., Muths, E., & Noon, B. R. (2012). The importance of local and landscape-scale processes to the occupancy of wetlands by pond-breeding amphibians.

 *Population Ecology, 54(4), 487-498.
- Semlitsch, R. D. (2003). Conservation of pond-breeding amphibians In R. D. Semlitsch (Ed.), *Amphibian Conservation*. Washington, D.C.: Smithsonian Institution.
- Senay, S. D., Worner, S. P., & Ikeda, T. (2013). Novel Three-Step Pseudo-Absence

 Selection Technique for Improved Species Distribution Modelling. *PLoS ONE*,

 8(8), 1-16. doi:10.1371/journal.pone.0071218
- Sinsch, U. (2014). Movement ecology of amphibians: from individual migratory behaviour to spatially structured populations in heterogeneous landscapes.

 Canadian Journal of Zoology, 92(6), 491-502. doi:10.1139/cjz-2013-0028
- Skelly, D. K., Freidenburg, L. K., & Kiesecker, J. M. (2002). Forest canopy and the performance of larval amphibians. *Ecology*, 83(4), 983.
- Skelly, D. K., Halverson, M. A., Freidenburg, L. K., & Urban, M. C. (2005). Canopy closure and amphibian diversity in forested wetlands. *Wetlands Ecology and Management*, 13(3), 261-269.
- Stephens, J. P., Berven, K. A., & Tiegs, S. D. (2013). Anthropogenic changes to leaf litter input affect the fitness of larval amphibian. *Freshwater Biology, online early*. doi:doi:10.1111/fwb.12155
- Steven, J. P., Miroslav, D., Jane, E., Catherine, H. G., Anthony, L., John, L., & Simon, F.
 (2009). Sample Selection Bias and Presence-Only Distribution Models:
 Implications for Background and Pseudo-Absence Data. *Ecological Applications*(1), 181.

- Stevenson, D. J., Cash, W. B., & Jensen, J. B. (2007, 2009). Gopher frog fact sheet.

 Retrieved from https://georgiawildlife.com/sites/default/files/wrd/pdf/fact-sheets/gopher_frog_2009.pdf
- Stoler, A. B., & Relyea, R. A. (2011). Living in the litter: the influence of tree leaf litter on wetland communities. *Oikos*, *120*, 862-872.
- The University of Georgia Center for Agribusiness and Economic Development. (2018.).

 2018 Ag Snapshots: A brief focus on Georgia's agricultural industry.
- Thurgate, N. Y., & Pechmann, J. H. K. (2007). Canopy Closure, Competition, and the Endangered Dusky Gopher Frog. *Journal of Wildlife Management*, 71(6), 1845-1852. doi:10.2193/2005-586
- U.S. Department of Agriculture. (2016.). Georgia's Land: Its Use and Condition, NaturalResources Conservation Service, Natural Resources Inventory, 4th Edition
- U.S. Fish and Wildlife Service. (2018). National Wetlands Inventory.
- U.S. Geological Survey. (2018). National Hydrography Dataset Plus, Version 2.
- Van Buskirk, J. (2005). Local and Landscape Influence on Amphibian Occurrence and Abundance. *Ecology*(7), 1936.
- Wells, K. D. (2007). Complex Life Cycles and the Ecology of AmphibianMetamorphosis *The Ecology and Behavior of Amphibians* (pp. 599-644).Chicago, Illinois: The University of Chicago Press.
- Werner, E. E. (1986). Amphibian metamorphosis: growth rate, predation risk, and optimal size at transformation. *American Naturalist*, *128*(3), 319-341.

- Werner, E. E. (1988). Size, scaling, and the evolution of complex life cycles. In B.

 Ebenman and L. Persson (Ed.), *Size-Structured Populations* (pp. 60-81). Berlin: Springer-Verlag.
- Wilbur, H. M. (1984). Complex life cycles and community organization in amphibians.
 Pages 195-224 in P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, editors. A
 New Ecology: Novel Approaches to Interactive Systems. Wiley, New York, New York, USA.
- Williams, B. K., Rittenhouse, T. A. G., & Semlitsch, R. D. (2008). Leaf litter input mediates tadpole performance across forest canopy gradients. *Oecologia*, 155, 377-384.
- Williams, B. K., Rittenhouse, T. A. G., & Semlitsch, R. D. (2008). Leaf litter input mediates tadpole performance across forest canopy gradiets. *Oecologia*, 155, 377-384.
- Zarnetske, P. L., Thomas C. Edwards, J., & Moisen, G. G. (2007). Habitat Classification Modeling with Incomplete Data: Pushing the Habitat Envelope. *Ecological Applications*(6), 1714.

Table 4.1: Estimated means and standard deviations of site and landscape variables measured for presence wetlands, or known Gopher frog ponds throughout Georgia, and wetlands in the pseudoabsence data set.

Descriptive data for variables measured at presence and pseudoabsence ponds Data source and predictor variables		pond				100m buffer				1km buffe	1km buffer		
		Presence		Pseudoabsence		Presence		Pseudoabsence		Presence		Pseudoabsence	
		mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Hydrology						'				'	_		
connected	1 = hydro connected, 0 = hydro isolated	0.18	0.39	0.22	0.42	NA		NA		NA		NA	
numwets	number of nearby wetlands	NA		NA		2.07	1.21	4.02	2.69	18.61	9.67	32.02	20.30
Land Cover	1												
nlcd11	% open water	11.37	29.16	2.91	12.00	3.64	9.94	1.26	4.22	0.71	1.33	1.38	5.91
nlcd21	% developed (low intensity)	2.51	10.81	1.39	7.20	4.05	7.24	2.43	4.46	3.94	1.77	3.06	3.63
nlcd2223	% developed (med-high intensity)	0.25	1.67	0.16	1.16	2.06	6.85	0.44	1.91	0.87	1.22	0.63	2.22
nlcd31	% barren land	0.00	0.00	0.17	1.61	0.00	0.00	0.53	3.36	0.57	2.40	0.80	3.32
nlcd41	% deciduous forest	6.21	21.16	2.44	7.59	7.03	13.56	6.54	13.13	7.30	8.35	6.82	10.05
nlcd4243	% evergreen & mixed forest	11.55	22.67	6.71	14.61	43.92	26.94	22.93	21.34	45.18	18.45	28.18	19.73
nlcd52	% shrub/scrub	4.42	14.20	2.04	11.01	6.38	9.98	5.60	10.17	8.58	7.99	8.10	10.44
nlcd71	% grasslands/herbaceous	10.34	25.17	1.26	4.48	13.41	20.93	4.77	11.00	11.01	14.26	5.90	6.54
nicd81	% pasture/hay	1.14	7.54	0.49	3.77	2.07	5.65	1.46	6.83	4.13	5.50	1.72	4.04
nlcd82	% cultivated crops	0.07	0.39	0.14	1.46	1.43	3.12	1.33	6.62	5.82	7.36	2.94	7.56
nlcd90	% woody wetlands	41.83	43.73	72.05	32.03	13.13	13.58	46.50	30.68	10.97	10.63	36.75	29.84
nlcd95	% emergent wetlands	10.32	24.42	10.25	20.88	2.87	6.92	6.20	14.51	0.90	1.49	3.72	8.03
Forest Structure	-												
covmax	mean % total cover	17.92	5.36	30.74	6.27	19.46	4.91	29.96	6.25	21.64	4.86	28.01	4.58
forbgrass	mean % forbs or grass cover	38.99	10.10	18.85	8.62	34.44	9.35	19.26	8.22	29.29	7.72	20.27	6.56
shrub	mean % shrub cover	24.62	5.17	32.20	5.51	24.83	4.83	31.78	5.09	27.65	4.46	30.91	3.82
Soil													
GT_soilsuit	Mean % Gopher tortoise soil suitability	NA		NA		0.36	0.15	0.18	0.13	0.44	0.14	0.24	0.16
¹ National Wetla	nds Inventory 2018 (U.S. Fish and	Wildlife Se	rvice. 2018										

³ National Landcover Database 2011 (Homer et al., 2015)

⁴ Forest Structure dataset (Tom Prebyl and Jeff Hepinstall-Cymerman, pers. comm.)

Gopher Tortoise Habitat Suitability Rating 2017 (v6.6) (National Resource Conservation Service, unpublished report)

Table 4.2: Eleven candidate models were developed using environmental predictors to explain Gopher frog presence at 42 wetlands in Georgia.

Model	forbgrass within pond ^a	grassland within 100m ^b	nearby wetlands within 100m °	Gopher tortoise soils within 100m ^d	Gopher tortoise soils within 1km ^e	evergreen and mixed forest within 1km ^f
null						
1	×					
2		×				
3	×	×	×			×
4	×		×	×		×
5	×	×	×	×		X
6		×	×	×		×
7	×	×		×		×
8	×	×	×	×		×
9	×	×			×	×
10			×		×	
11				×		

^a The coverage of forbs and grass within a pond serves as a proxy for an intermediate hydroperiod and relatively low canopy cover, both of which are important for gopher frog larval growth and survival.

^b Higher proportions of grassland/herbaceous land cover within the 100m buffer suggests that the pond is embedded in a terrestrial community with low canopy cover, a characteristic that suggests it is a fire-maintained habitat preferred by Gopher frogs.

^c Clustered arrangements of wetlands within 100 meters of the pond should increase opportunities for Gopher frog dispersal and migration.

^d Suitable Gopher tortoise soils within 100 meters of the pond suggest that tortoises may be present, and their burrows provide safe refuges for Gopher frogs near the pond.

^e Suitable Gopher tortoise soils within 1 kilometer of the pond suggest that tortoises may be present in nearby patches, and Gopher frogs will travel distances up to 1 kilometer or more between burrows and ponds.

^f Higher proportions of pine-mixed-hardwood forests within 1 kilometer would include varied upland habitat types reportedly used by Gopher frogs.

Table 4.3: Habitat suitability model selection results including the number of parameters (K), Akaike's Information Criterion for small sample sizes (AICc), ΔAICc, model weight (w), and cumulative model weight. Models were ranked by AICc (Burnham & Anderson, 2002).

Model	K	AICc	ΔAICc	W	Cumulative w
4	4	74.63	0	0.44	0.44
5	5	75.54	0.91	0.28	0.73
7	4	76.94	2.31	0.14	0.87
9	4	78.06	3.43	0.08	0.96
8	4	79.14	4.51	0.05	0.99
3	4	86.05	11.42	0.00	1.00
1	1	97.45	22.82	0.00	1.00
6	4	111.93	37.3	0.00	1.00
10	2	122.82	48.2	0.00	1.00
11	1	137.43	62.8	0.00	1.00
2	1	174.2	99.58	0.00	1.00
null model	0	181.45	106.82	0.00	1.00

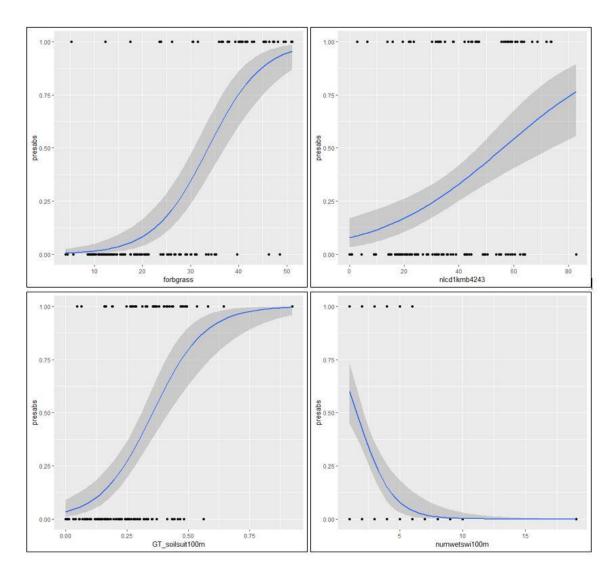


Figure 4.1: Relationships between explanatory variables used in the model and Gopher frog presence. Forbs/grass within the pond and Evergreen-mixed forest are represented as proportions of land cover within the pond and within 1 km of the pond respectively. The Number of wetlands within 100m of the pond is represented with number of wetlands on the x-axis. Gopher tortoise soil suitability within 100 m is represented as an index 0-1.

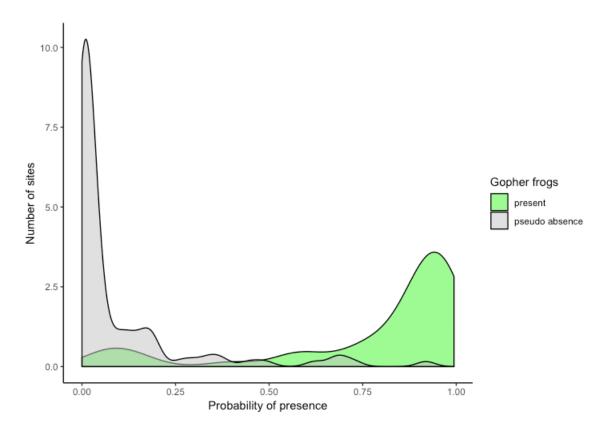


Figure 4.2. Density plots of model predicted probabilities of Gopher frog presence [habitat suitability] among all known present versus pseudoabsence ponds.

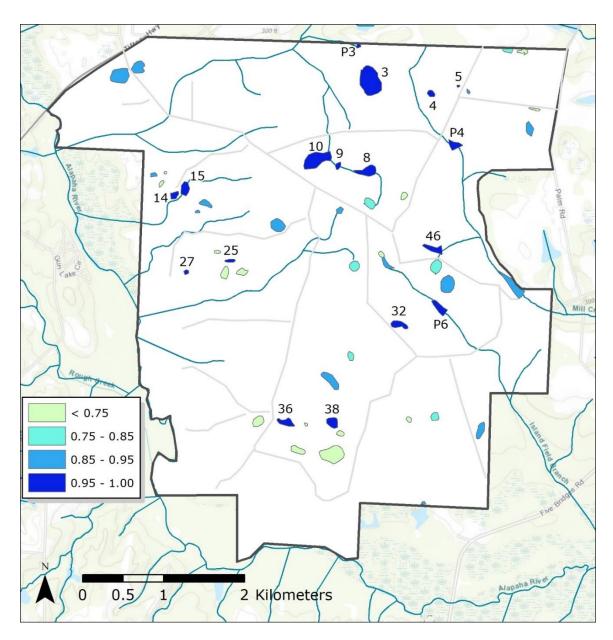


Figure 4.3: Habitat suitability for the Gopher frog at Alapaha River Wildlife Management Area, as predicted by the top performing model, #4.

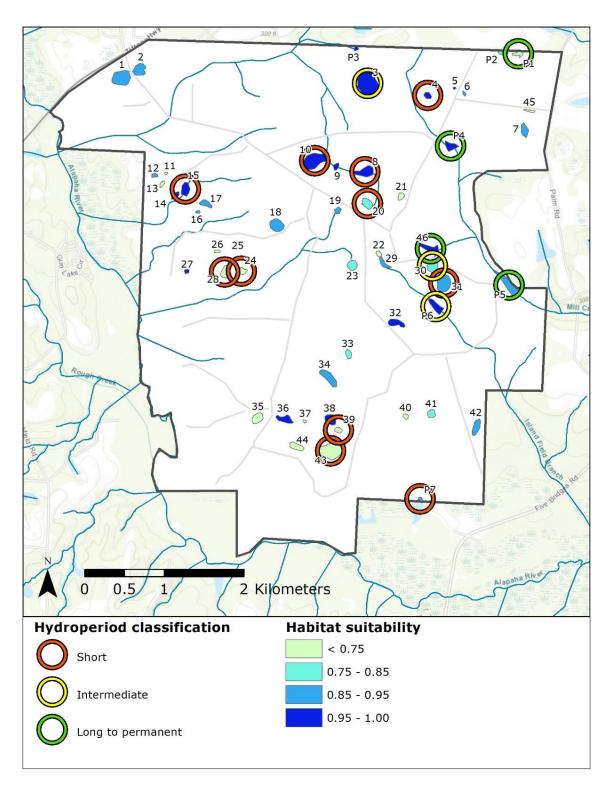


Figure 4.4: The habitat suitability map for Alapaha ponds with an overlay of the hydroperiod classifications for a suite of ponds.

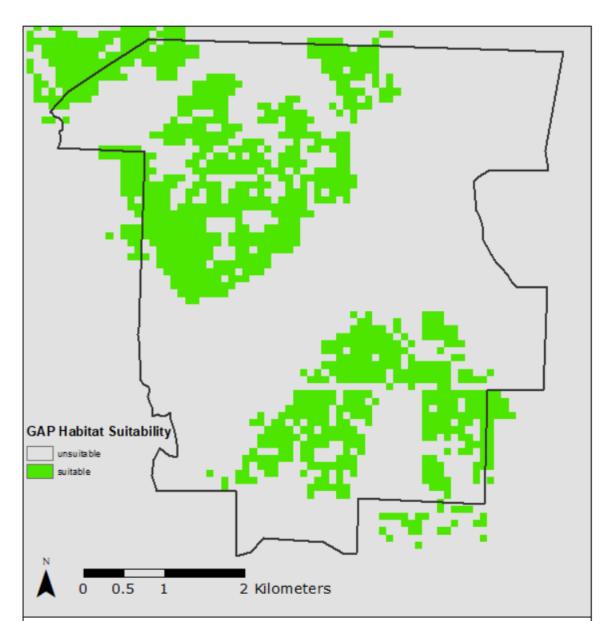


Figure 4.5: The Georgia GAP Analysis distribution model of suitable habitat for the Gopher frog in the Alapaha River Wildlife Management Area. Binary output predicts suitable habitat in green and unsuitable habitat in gray.

CHAPTER 5

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The purpose of this study was to investigate habitat associations of Gopher frogs to determine which habitat attributes are most important to population persistence within managed landscapes. Conservation strategies for recovering Gopher frog populations include activities such as captive breeding and rearing, reintroduction, population supplementation, monitoring and adaptive management, and habitat restoration, but the success of these efforts will depend on the appropriate selection of sites that are most likely to promote long-term persistence of Gopher frog populations.

At ARWMA, I estimated occupancy of Gopher frogs and other pond-breeding amphibians at a suite of wetlands, and I evaluated wetland conditions and how variables such as hydroperiod, canopy cover, and isolation may impact suitability of sites for Gopher frogs. I recorded hydroperiod data for ARWMA wetlands during my field season and used these data to develop a technique to remotely identify wetlands with intermediate-to-long hydroperiods using a provisional data set of remote sensing products. Using gopher frog occurrence data from the Georgia Department of Natural Resources, I developed a habitat suitability model that predicts potential breeding wetlands for Gopher frogs using habitat attributes collected at the pond, local wetland context, and landscape scale and projected it over ARWMA.

The findings of my field surveys and occupancy studies from 2016-2017 at ARWMA suggest that Gopher frogs may currently be restricted to a single breeding pond

on the property. Pond 3 is an emergent herbaceous wetland that occurs within a power line clearing. Historic aerial photographs confirm its former condition as part of a larger forested cypress-gum pond, but a power line clearing bisecting this pond sometime between 1948 and 1962 resulted in its conversion to its current open-canopied condition, which is maintained by ongoing management of the power line easement. Based on the isolated, non-overlapping calls, few detections, and no detections of tadpoles, the current population size at pond 3 is likely small. ARWMA has few natural ponds that have intermediate-to-semipermanent hydroperiods, and in 2016-2017, I observed only 4 of the 24 study ponds to remain inundated through April; these included two artificial ponds where fish were detected.

Management guidelines for pond-breeding amphibians advocate for the protection of a mosaic of wetlands of variable hydroperiods across a landscape to allow for breeding in most years regardless of stochastic environmental conditions (Greenberg, Goodrick, Austin, & Parresol, 2015; Semlitsch, 2000). While pond-breeding amphibians exhibit dramatic fluctuations in population size and are adapted to dynamic environments, a population will require at least one successful breeding event within its lifetime to remain stable (Jones, McLaughlin, Henson, Haas, & Kaplan, 2018; Snodgrass, Komoroski, Jr, & Burger, 2000). Climate projections for the southeastern United States predict that hydroperiods will become shorter in ephemeral wetlands. Particularly in sandhills habitat, climate-induced drought will threaten the recovery of many pond-breeding amphibian populations (Bates, Kundzewicz, Wu, & Palutikof, 2008; Greenberg et al., 2015). With few intermediate-to-long hydroperiod wetlands identified at ARWMA, additional efforts should be made to increase wetland hydroperiods.

Modification of wetlands was common across ARWMA, with many natural ponds connected by ditches, encircled by deeply ditched fire breaks, or overplanted with slash pine encroaching into the pond basin. In addition to these direct impacts on wetland hydrology, the conversion to pine plantation forestry in the uplands has likely interfered with historic inundation patterns, contributing to shorter hydroperiods for wetlands at ARWMA. Pond restoration objectives for recovering Gopher frog and other pondbreeding amphibian populations at ARWMA should include eliminating ditches, removing hardwoods and pines from pond basins, and reducing tree densities in the surrounding uplands to extend the hydroperiod of targeted wetlands (Bryant, Bhat, & Jacobs, 2005; Freeman & Jose, 2009; Jones et al., 2018; Klaassen, 2001; Lu, Sun, McNulty, & Comerford, 2009; Marsh & Trenham, 2001; Skelly, Freidenburg, & Kiesecker, 2002; Thurgate & Pechmann, 2007). The habitat suitability model identified ponds 10 and 8 as having > 0.98 probability of Gopher frog presence, but a ditch currently connecting these ponds to two other ponds has altered their hydrology. The DSWE hydroperiod analysis predicted both ponds as having short hydroperiods in 2015 and 2016, and field surveys confirmed short and flashy hydroperiods with irregular filling and drying for both of these ponds in 2017. Removal of this ditch may allow the ponds to experience longer and continuous hydroperiods that are of sufficient length to support Gopher frog recruitment. Removal of the trees and shrubs that have established within the ponds would contribute to an increase in hydroperiod, while promoting herbaceous growth within the basin which benefits larval amphibians.

Increasing fire frequency within wetlands will also increase habitat suitability for Gopher frogs and other pond-breeding amphibians. Hard firebreaks surrounding wetlands

disturb the ecotone and alter the hydrology of the basin and should be removed to allow fire to move through wetlands. If firebreaks must be maintained within the wetland ecotone, raking and weed-eating provide alternative management options to plowed firebreaks (P. Hill, Florida Fish and Wildlife Conservation Commission, pers. comm). Including wetlands within burn units and scheduling burns for times of year when the wetlands have dried can increase wetland hydroperiod and improve conditions for larval amphibians. Growing season fires prevent woody encroachment of shrubs and trees within the wetland, while maintaining deeper basins by burning organic matter and sediments and creating structural heterogeneity in wetland vegetation (P. Hill, Florida Fish and Wildlife Conservation Commission, pers. comm). The basin of pond 3, the pond where Gopher frogs were detected, is comprised of dense stands of maidencane (*Panicum hemitomon*). While a valuable wetland plant and an indicator species for Gopher frogs, it can become weedy, forming dense, monotypic stands (Holm & Sasser, 2008) that shade out previously open spaces within the water column and limit the penetration of sunlight and algal growth that are required by developing amphibian larvae (P. Hill, Florida Fish and Wildlife Conservation Commission, pers. comm). Burning pond 3 when it is dry would deepen the pond basin and create structural heterogeneity in wetland vegetation that would limit the clonal spread of maidencane. Additional measures to recover Gopher frog populations at pond 3 could include limiting vehicular access to the power line clearing during the breeding season and through spring. Doing so may help limit direct mortality to adult and post-metamorphic frogs which often travel along dirt roads and other cleared trails. Fewer ruts and impacts to roads and paths adjacent to ponds will also help maintain the vegetation and the integrity of the basin and facilitate the movement of

water into the basin, rather than allowing it to pool in ruts and ditches. A gate installed at the powerline right of way would likely provide increased protection to gopher frogs.

Other priority wetlands for management activities include ponds 46 and 32. Pond 46 is an impoundment which supported the greatest number of amphibian species at ARWMA in 2016-2017 (Chapter 2, Table 2.3). It is the only one of the study ponds which had > 0.95 predicted suitability, a long-to-semipermanent hydroperiod, and did not host fish. While it is not hydrologically isolated, it likely dries in most years (Ch 4, Table 3.6, Table 3.7), and no fish were detected during 2016-2017 field surveys. Restoration of this pond to support Gopher frog populations would likely require intensive reshaping of the basin to establish appropriate vegetation and create a shallow littoral zone, but it is already valuable habitat to many other pond-breeding amphibians in its current state (Baldwin, Calhoun, & deMaynadier, 2006). So long as this pond is not stocked with fish, it should continue to support a diversity of pond-breeding amphibians at ARWMA (Bailey, Holmes, Buhlmann, & Mitchell, 2006). Pond 32's predicted suitability for Gopher frogs was 0.992. It was not included in my 2016-2017 field surveys, but I visited it twice and believe it to have a short hydroperiod; it was not inundated on either of my visits, and the DSWE analysis predicted it to be wet in only two scenes for 2016 (Chapter 3, Table 3.6). However, as a relatively small wetland, it is likely to be more responsive to management actions which may increase hydroperiod, including thinning and burning in the uplands and in the pond basin. All of these ponds for which I've suggested management focus are situated in the northeastern quadrant of ARWMA where Gopher frogs have previously been detected. Wetland restoration activities in this part of the

property, along with continued management for Gopher tortoises in the surrounding uplands, are most likely to benefit ARWMA's resident Gopher frog population.

Restoration efforts without population supplementation may be insufficient to recover the Gopher frog population at ARWMA. While hydroperiods of some targeted wetlands may be restored quickly, facilitated dispersal, or translocation, of captively reared Gopher frogs to newly restored sites may be necessary and would increase chances of population persistence. Several years of releases accompanied by both short-term and long-term monitoring of reintroduced populations is recommended.

Literature Cited

- Bailey, M. A., Holmes, J. N., Buhlmann, K. A., & Mitchell, J. C. (2006). Habitat management guidelines for amphibians and reptiles of the southeastern United States *Partners in Amphibian and Reptile Conservation Technical Publication HMG-2*. Montgomery, Alabama.
- Baldwin, R. F., Calhoun, A. J. K., & deMaynadier, P. G. (2006). The significance of hydroperiod and stand maturity for pool-breeding amphibians in forested landscapes. *Canadian Journal of Zoology*(11), 1604.
- Bates, B. C., Kundzewicz, Z. W., Wu, S., & Palutikof, J. P. (2008). *Climate Change and Water* In Intergovernmental Panel on Climate Change (Ed.), *IPCC Technical Paper VI*.
- Bryant, M. L., Bhat, S., & Jacobs, J. M. (2005). Measurements and modeling of throughfall variability for five forest communities in the Southeastern US. *Journal of Hydrology*, 312(1-4), 95-108. doi:10.1016/j.jhydrol.2005.02.012
- Freeman, J. E., & Jose, S. (2009). The role of herbicide in savanna restoration: Effects of shrub reduction treatments on the understory and overstory of a longleaf pine flatwoods. *Forest Ecology and Management*, 257, 978-986.

 doi:10.1016/j.foreco.2008.10.041
- Greenberg, C. H., Goodrick, S., Austin, J. D., & Parresol, B. R. (2015). Hydroregime

 Prediction Models for Ephemeral Groundwater-Driven Sinkhole Wetlands: a

 Planning Tool for Climate Change and Amphibian Conservation. *Wetlands*, 35(5),
 899-911.

- Holm, G. O., & Sasser, C. E. (2008). The Management and Ecology of the Wetland Grass, Maidencane. *Journal of Aquatic Plant Management*, 46(46), 51-60.
- Jones, C. N., McLaughlin, D. L., Henson, K., Haas, C. A., & Kaplan, D. A. (2018). From salamanders to greenhouse gases: does upland management affect wetland functions? *Frontiers in Ecology and the Environment*, 16(1), 14-19.
- Klaassen, W. (2001). Evaporation from rain-wetted forest in relation to canopy wetness, canopy cover, and net radiation. *Water Resources Research*, 37(12), 3227-3236. doi:10.1029/2001WR000480
- Lu, J., Sun, G., McNulty, S. G., & Comerford, N. B. (2009). Sensitivity of pine flatwoods hydrology to climate change and forest management in Florida, USA, *Wetlands*, 29(3), 826–836
- Marsh, D. M., & Trenham, P. C. (2001). Metapopulation Dynamics and Amphibian Conservation. *Conservation Biology*(1), 40.
- Semlitsch, R. D. (2000). Principles for management of aquatic breedingamphibians. *Journal of Wildlife Management*, 64, 615-631.
- Skelly, D. K., Freidenburg, L. K., & Kiesecker, J. M. (2002). Forest canopy and the performance of larval amphibians. *Ecology*, 83(4), 983.
- Snodgrass, J. W., Komoroski, M. J., Jr, A. L. B., & Burger, J. (2000). Relationships among Isolated Wetland Size, Hydroperiod, and Amphibian Species Richness: Implications for Wetland Regulations. *Conservation Biology*, *14*(2), 414-419.
- Thurgate, N. Y., & Pechmann, J. H. K. (2007). Canopy Closure, Competition, and the Endangered Dusky Gopher Frog. *Journal of Wildlife Management*, 71(6), 1845-1852. doi:10.2193/2005-586

Appendix 3.1: Dynamic Surface Water Extent (DSWE) algorithm used in Hydroperiod estimation.

This is the algorithm description derived from the prototype implementation provided by the authors and subsequent conversations and emails.

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Algorithm Description - Overview:

The algorithm relies on a series of relatively simple and efficient water detection tests, each with their own output code for a "positive" test result or 0 for a negative test result. Resulting in a 5 digit output value in the range 00000 to 11111, where each digit corresponds to a specific test.

These test results are then further refined (recoded) to the following values:

- 0 -> Not Water
- 1 -> Water High Confidence
- 2 -> Water Moderate Confidence
- 3 -> Partial Surface Water Pixel
- 9 -> Cloud, Cloud Shadow, or Snow
- 255 -> Fill (no data)

The algorithm provides an output of 3 files. The first file represents the Raw DSWE (recoded values 0, 1, 2, 3, and 255; sceneid_dswe_raw.tif). The second represents the Raw DSWE with filtering applied for Cloud and Cloud Shadow (recoded values 0, 1, 2, 3, 9, and 255; sceneid_dswe_ccs.tif). The third represents the Raw DSWE with filtering applied for Percent-Slope, Cloud, Cloud Shadow, or Snow (recoded values 0, 1, 2, 3, 9, and 255; sceneid_dswe_psccs.tif).

Percent-Slope is utilized to remove locations where the terrain is too sloped to hold water. Any values that meet this criteria are recoded to a value of 0.

Algorithm Description - Inputs:

Primary source of the input is Surface Reflectance derived from L1T products.

Specifically the Blue, Green, Red, NIR, SWIR1, and SWIR2 Surface Reflectance bands, along with the CFmask band.

A DEM is also utilized to generate an internal Percent-Slope band for the required slope filtering.

Algorithm Description - Detailed:

NOTE: Keep in mind during the processing of the Raw DSWE band, the output is filtered for fill data and those values are set to 255.

Raw DSWE -> Output:

1) Calculate Modified Normalized Difference Wetness Index (MNDWI) from the Green and SWIR1 bands.

mndwi = (Green - SWIR1) / (Green + SWIR1)

2) Calculate Multi-band Spectral Relationship Visible (MBSRV) from the Green and Red bands.

mbsrv = Green + Red

3) Calculate Multi-band Spectral Relationship Near-Infrared (MBSRN) from the NIR and SWIR1 bands.

mbsrn = NIR + SWIR1

4) Calculate Automated Water Extent Shadow (AWEsh) from the Blue, Green, and SWIR2 bands, along with MBSRN.

awesh = (Blue)

+ (2.5 * Green)

+ (-1.5 * mbsrn)

+ (-0.25 * SWIR2))

5) Perform the first test by comparing the MNDWI to a Wetness Index threshold; Where the threshold ranges from 0.0 to 2.0 and is defaulted to a value of 0.0123.

if (mndwi > 0.0123) set the ones digit (Example 00001)

- 6) Perform the second test by comparing the MBSRV and MBSRN values to each other. if (mbsrv > mbsrn) set the tens digit (Example 00010)
- 7) Perform the third test by comparing AWEsh to an Automated Water Extent Shadow threshold; Where the threshold ranges from -2.0 to 2.0 and is defaulted to a value of 0.0. if (awesh > 0.0) set the hundreds digit (Example 00100)
- 8) Perform the fourth test by comparing the MNDWI along with the NIR and SWIR1 bands to the following thresholds. Partial Surface Water Test-1 threshold; Where the threshold ranges from -2.0 to 2.0 and is defaulted to a value of -0.5. Partial Surface Water

Test-1 NIR threshold; Where the threshold ranges from 0 to data maximum and is defaulted to a value of 1500. Partial Surface Water Test-1 SWIR1 threshold; Where the threshold ranges from 0 to data maximum and is defaulted to a value of 1000.

if (mndwi > -0.5)

&& SWIR1 < 1000

&& NIR < 1500) set the thousands digit (Example 01000)

9) Perform the fifth test by comparing the MNDWI along with the NIR and SWIR2 bands to the following thresholds. Partial Surface Water Test-2 threshold; Where the threshold ranges from -2.0 to 2.0 and is defaulted to a value of -0.5. Partial Surface Water Test-2 NIR threshold; Where the threshold ranges from 0 to data maximum and is defaulted to a value of 1700. Partial Surface Water Test-2 SWIR2 threshold; Where the threshold ranges from 0 to data maximum and is defaulted to a value of 650.

if (mndwi > -0.5)

&& SWIR2 < 1000

&& NIR < 2000) set the ten-thousands digit (Example 10000)

10) Recode the results from the previous steps using the following ranges and values.

11001 11111 : 1 (Water - High Confidence)

10111 10999:1

01111 01111 : 1

11000 11000 : 3 (Partial Surface Water Pixel)

10000 10000 : 3

 $01000\ 01000:3$

10012 10110 : 2 (Water - Moderate Confidence)

10011 10011:2

10001 10010:2

01001 01110 : 2

00010 00111:2

00000 00009 : 0 (Not Water)

11) Output the Raw DSWE

Raw DSWE -> Cloud, Cloud Shadow, or Snow -> Output:

1) Perform a test by comparing CFmask band to the Cloud, Cloud Shadow, and Snow values.

if (cfmask == 2 or cfmask == 4 or cfmask == 3) set the cloud/cloud shadow/snow filtered Raw DSWE to a recoded value of 9, otherwise set to Raw DSWE

2) Output the Cloud, Cloud Shadow, and Snow filtered Raw DSWE.

Raw DSWE -> Percent-Slope -> Cloud, Cloud Shadow, or Snow -> Output:

- 1) Build a Percent-Slope band from the DEM source.
- 2) Perform a test by comparing the Percent-Slope band to a Percent-Slope threshold; where the threshold ranges from 0.0 to 100.0 and is defaulted to a value of 6.0. if (percent-slope >= 6.0) set the Percent-Slope filtered Raw DSWE to a recoded value of 0, otherwise set to Raw DSWE
- 3) Perform a test by comparing CFmask band to the Cloud and Cloud Shadow values. if (cfmask == 2 or cfmask == 4 or cfmask == 3) set the Percent-Slope filtered Raw DSWE to a recoded value of 9, otherwise leave alone
- 4) Output the Percent-Slope, Cloud, Cloud Shadow, and Snow filtered Raw DSWE.

1. Reclassify 7 DWSE layers in

E:\Erin\ModelBuilderHydro_Results\DSWEinputs2017.gdb (jeff's copy on external hard drive of the data on her now-dead Dell 3500), 3 > 1, all others to 0, 7 times. One example of the code below:

arcpy.gp.RasterCalculator_sa('Con("DSWE20170304" == 3,1,0)',
"E:/Erin/ModelBuilderHydro_Results/DSWEinputs2017.gdb/DSWE20170115_rc3_t
o1")

- 2. Zonalstats, stat = MAX value, will report if there are any 1's within the zones, in this case **E:\Erin\AlapahaHydroperiod.gdb\alapaha_discrete_wetlands**, one example below:
- # Replace a layer/table view name with a path to a dataset (which can be a layer file) or create the layer/table view within the script
- # The following inputs are layers or table views: "alapaha_discrete_wetlands",

arcpy.gp.ZonalStatisticsAsTable_sa("alapaha_discrete_wetlands", "Id",

"DSWE20170507_rc3_to1",

"DSWE20170507_rc3_to1"

"E:/Erin/ModelBuilderHydro_Results/DSWEinputs2017.gdb/alapaha_discrete_wetla nds_x_DWSE20170507_cl3_max", "DATA", "MAXIMUM")

 Add 7 new fields to alapha_discrete_wetlands, wet#### where #### = 4 digit month-day code

- 4. Join each zonalstats output file to the alapha_discrete_wetlands attribute table by ID
- 5. Field Calculator in vector attribute table to copy the MAX value in each zonalstats table into the appropriate field in vector layer
- 6. Remove all joins, repeat steps 4-5 7 total times
- 7. Copy alapha_discrete_wetlands to a new geodatabase, *Erin_traveling* and feature class, alapha_dis_wet_with_DSWE_3s

Appendix 4.1: Predicted habitat suitability of ponds at Alapaha for Gopher frogs, ranked by highest suitability to lowest suitability, as predicted by the top habitat suitability model, glm4.

Pond ID	suitability	SE
3	0.99681	0.004182
4	0.99336	0.00811
15	0.992942	0.007994
32	0.992535	0.008071
5	0.99247	0.007969
27	0.990007	0.010525
25	0.988694	0.012372
P4	0.986021	0.013054
8	0.984552	0.015109
10	0.981447	0.017682
P6	0.98109	0.019071
P3	0.976307	0.025625
14	0.97445	0.021277
36	0.970477	0.020327
9	0.963646	0.027439
46	0.954378	0.040699
38	0.952315	0.034713
29	0.948696	0.040976
18	0.937986	0.047281
34	0.936206	0.037608
P7	0.934255	0.040558
1	0.927143	0.042816
42	0.924695	0.058487
17	0.918812	0.056926
2	0.9105	0.065925
P5	0.908008	0.063084
16	0.901135	0.063014
7	0.89404	0.053935
19	0.889717	0.100858
31	0.88033	0.089326
12	0.862656	0.112692
6	0.859371	0.140615
41	0.83691	0.110522
33	0.832064	0.122419
30	0.81875	0.088826
20	0.788218	0.112282

Pond ID	suitability	SE
P2	0.773169	0.137939
23	0.766777	0.117124
35	0.736189	0.115867
24	0.682443	0.134185
13	0.661959	0.259021
11	0.661896	0.220517
40	0.520701	0.192917
44	0.489599	0.241704
P1	0.482404	0.206002
21	0.384961	0.194379
45	0.375449	0.203905
26	0.374772	0.201877
39	0.311722	0.136896
43	0.272553	0.186287
22	0.238848	0.096508
28	0.026186	0.023561