# IF YOU BUILD IT, WILL THEY COME? ESTIMATING SQUAMATE RESPONSES TO PINE SAVANNA RESTORATION

by

Alexandra Brown

(Under the Direction of John C. Maerz)

## ABSTRACT

Herpetofauna are notoriously difficult to monitor, and efficient monitoring techniques for these species are desperately needed to inform management actions. I evaluated the effectiveness of wildlife cameras for detecting two representative species of herpetofauna (snakes and frogs) and determined the influence of individual characteristics on detectability. I used these results to develop a series of wildlife camera arrays to monitor the impact of pine savanna restoration on the squamate community at Alapaha River Wildlife Management Area (ARWMA), which has resident populations of several snakes identified as species of greatest conservation need in Georgia's State Wildlife Action Plan. Wildlife cameras were 7 times more efficient at detecting herpetofauna than traditional survey methods; however, detection rates varied between models and depended on surface temperature differential and, in some cases, body size. The response of squamates to restoration actions on ARWMA and the temporal scale at which these responses became evident appeared to be highly species dependent.

INDEX WORDS: snake; frog; lizard; wildlife camera; monitoring; detection probability; pine savanna restoration; hierarchical occupancy model; management

# IF YOU BUILD IT, WILL THEY COME? ESTIMATING SQUAMATE RESPONSES TO PINE SAVANNA RESTORATION

by

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# DEDICATION

I dedicate this thesis to my parents, Carol and Eric Brown. They fostered a love for all animals that started me on the path to where I am today. Thank you for your support and encouragement of my goals.

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# TABLE OF CONTENTS

APPENDICES

# LIST OF TABLES

# LIST OF FIGURES

Page

# CHAPTER 1

# INTRODUCTION

Habitat loss endures as one of the greatest past, present, and future drivers of biodiversity decline, with much of this loss driven by human activity (Brooks et al. 2002; Pereira et al. 2010). Recent estimates indicate that humans have directly modified over 50% of Earth's land surface, compounded by the indirect effects of these activities on surrounding landscapes (Hooke et al. 2013). Despite being widespread, the deleterious effects of habitat loss on species have the potential to be controlled and reduced provided substantial action is taken.

The field of restoration ecology emerged in response to anthropogenic land use change as a method of "assisting the recovery of ecosystems that have been damaged, degraded, or destroyed" (Society for Ecological Restoration 2004). While ecological restoration has the potential to increase the amount of available habitat, there are implicit assumptions associated with attempting to recreate a system that formed over the course of centuries in a matter of months or years. The failure to recognize and address these assumptions (i.e., myths about the ability to create exact copies of historic ecosystems by recreating plant communities, utilization of standardized methods in inappropriate situations, etc.) can lead to unsatisfactory results (Hilderbrand et al. 2005). The Field of Dreams Hypothesis (Palmer et al. 1997) is one such assumption that shapes many restoration projects. This hypothesis posits that animals independently recolonize restored areas following the re-establishment of vegetation, returning to pre-disturbance population and community dynamics (Frick et al. 2004, McAlpine et al. 2016). This hypothesis, while seemingly ubiquitous throughout restoration practice, has not been extensively tested and fails to acknowledge the plant-animal interactions critical to ecosystem function (Cross et al. 2019, Tomlinson et al. 2014). Therefore, more work is needed to understand the effectiveness of vegetation-based restoration for organisms and ecosystems targeted by these initiatives.

Several factors likely determine whether fauna responds to habitat restoration. One is external biogeographic processes such as the extent of isolation of restored habitats from potential source populations (Lehtinen and Galatowitsch 2001). A second factor is the extent to which restoration and ongoing management recreate essential conditions that support some species (Nichols and Grant 2007). For example, snake species such as the federally petitioned eastern diamondback rattlesnake (*Crotalus adamanteus*) require specific disturbance regimes (Hoss et al. 2010) and the presence of keystone species to provide habitat features that allow them to survive disturbance, extreme weather, and shifting climate. Third is the extent to which legacies of historic land use affect the performance of species within restored areas (Burrow et al. 2021). Effective restoration and conservation require evaluating the relative importance of extrinsic biogeographic and intrinsic habitat factors that limit the recovery of animal species within restored habitats. Upon evaluating these factors, land managers may ultimately have to identify additional actions such as assisted migration to complement habitat management on restored sites (Cristescu et al. 2013). However, to evaluate the impact of these factors and determine what species remain, populations of target fauna that land managers want to recover must be monitored.

Reptiles are undergoing global declines, predominantly due to human-induced habitat loss, with as many as 33% of reptile species threatened with extinction globally (Böhm et al. 2013). Despite the widespread and severe decline of reptiles, restoration monitoring efforts rarely measure the responses of reptile species to management actions (Munro et al. 2007, Todd et al.

2010). Among all reptile species, information on snake colonization and utilization of restored habitats remains particularly sparse (Nichols and Grant 2007). Snakes are a notoriously difficult group to survey due to their cryptic nature and low activity rate, compounded by the heavily seasonal activity patterns of many herpetofauna (Böhm et al. 2013, Mazorelle et al. 2007, Steen 2010). Consequently, there is often a lack of robust information about snake responses to habitat restoration and management which can impede conservation efforts (Gibbons et al. 2000). Identifying improved methods for surveying snake communities that minimize effort and bias while increasing detection rate would allow land managers to determine the impact of conservation and management actions on snake species.

### *Longleaf Pine Restoration*

Pine savannas such as the longleaf pine (*Pinus palustris*) ecosystem historically covered vast swaths of the southeastern United States. The less than 3% of old-growth longleaf pine habitat remaining now exists as relatively small, isolated "islands" supporting high levels of endemic biodiversity separated by "oceans" of developed land unsuitable for many native species (Brockway et al. 2007). Pine savanna restoration has become a major conservation focus across the southeastern United States; however, these projects focus primarily on plant community restoration with targeted goals for select fauna such as the Gopher tortoise (*Gopherus polyphemus*) and Red-cockaded woodpecker (*Picoides borealis*). Though it is believed that habitat restoration for these umbrella species will benefit other flora and fauna, the responses of additional taxa are rarely monitored and therefore uncertain (Branton and Richardson 2011). As a result, there is a general lack of knowledge about the way that many species respond to pine savanna restoration. Such knowledge would be useful in evaluating the impact of restoration initiatives and guiding efforts to increase the positive effects of restoration for other non-target taxa.

The longleaf pine ecosystem harbors a diverse suite of amphibian and reptile species (Guyer and Bailey 1993). These species perform a variety of ecological roles including herbivore, detritivore, predator, prey, and seed disperser (Guyer and Bailey 1993, Böhm et al. 2013). Of the 29 snake species characteristic of longleaf pine savannas, nine are specialists whose ranges extensively overlap with that of longleaf pine ecosystems (Howze and Smith 2021, Means 2007). Therefore, longleaf pine restoration efforts have the potential to heavily impact herpetofauna conservation, even in situations where they are not the target species. To benefit herpetofauna, however, their responses to general management actions require further investigation. Previous studies of the impact of longleaf pine restoration have focused generally on the entire reptile community or on the specific tracking of a single focal species (Steen et al. 2013, Howze and Smith 2021). The more general attempts to evaluate community-wide responses to restoration were typically conducted for only a portion of the year and may miss seasonal windows of activity (Ryberg et al. 2021) or use methods biased for certain species (Enge 2001). By potentially biasing results and obscuring important responses among some species, these deficiencies could lead to misguided management decisions or a lost opportunity to conserve a wider suite of species when restoring longleaf pine habitat.

### *Thesis Objectives*

The objectives of this thesis were to (1) determine the detection rate of snakes and frogs using different wildlife cameras and evaluate the influence of environmental and individual factors on the effectiveness of the cameras for passively sampling herpetofauna populations, and (2) estimate patch occupancy rates for the squamate assemblage at Alapaha River Wildlife

Management Area (ARWMA) to determine whether current longleaf pine restoration efforts improve site occupancy for non-target species. The thesis is divided into four chapters (including this introduction). Chapters 2 and 3 are written as manuscripts to be submitted for publication. Chapter 2 describes the development and testing of modified inverted bucket housing units with various wildlife camera models for the passive monitoring of herpetofauna. I estimate detection rates of the various cameras and snake species ex-situ using wild and captive snakes native to Georgia. This allowed me to determine which camera model would be used in the squamate community survey described in Chapter 3. I then determine how factors such as body size and surface temperature differential influence the detection of different individuals during each trial. Chapter 3 presents a year-long study of the squamate assemblage at several sites undergoing active habitat restoration. I estimate squamate community use and the richness of squamates at ARWMA in historic sites, unrestored sites, and restored sites of various ages. I then use a hierarchical Bayesian community occupancy model to estimate the occupancy probability of sites based on distance from the historic site, time since thinning, time since burning, and pine basal area. Chapter 4 summarizes the findings of the thesis and potential applications of the findings to herpetofauna monitoring and conservation efforts.

# Literature Cited

Böhm, M., Collen, B., Baillie, J. E., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffman, M., Livingstone, S. R., Ram, M., Rhodin, A. G. J., Stuart, S. N., van Dijk, P. P., Young, B. E., Afuang, L. E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., Akarsu, F., Alencar, L. R. V., Allison, A., Ananjeva, N., Anderson, S., Andrén, C., Ariano- Sánchez, D., Arredondo, J. C., Auliya, M., Austin, C. C., Avci, A., Baker, P. J., Barreto-Lima, A. F., Barrio-Amorós, C. L., Basu, D., Bates, M. F., Batistella, A., Bauer, A., Bennett, D., Böhme, W., Broadley, D., Brown, R., Burgess, J., Captain, A., Carreira, S., Castañeda, M. R., Castro, F., Catenazzi, A., Cedeño-Vázquez, J. R., Chapple, D. G., Cheylan, M., Cisneros-Heredia, D. F., Cogalniceanu, D., Cogger, H., Corti, C., Costa, G. C., Couper, P. J., Courtney, T., Crnobrnja-Isailovic, J., Crochet, P. -A., Crother, B., Cruz, F., Daltry, J. C., Daniels, R. J. R., Das, I., de Silva, A., Diesmos, A. C., Dirksen, L., Doan, T. M., Dodd Jr., C. K., Doody, J. S., Dorcas, M. E., Duarte de Barros Filho, J., Egan, V. T., El Mouden, E. H., Embert, D., Espinoza, R. E., Fallabrino, A., Feng, X., Feng, Z. -J., Fitzgerald, L., Flores-Villela, O., França, F. G. R., Frost, D., Gadsden, H., Gamble, T., Ganesh, S. R., Garcia, M. A., García-Pérez, J. E., Gatus, J., Gaulke, M., Geniez, P., Georges, A., Gerlach, J., Goldberg, S., Gonzalez, J. -C. T., Gower, D. J., Grant, T., Greenbaum, E., Grieco, C., Guo, P., Hamilton, A. M., Hare, K., Hedges, S. B., Heideman, N., Hilton-Taylor, C., Hitchmough, R., Hollingsworth, B., Hutchinson, M., Ineich, I., Iverson, J., Jaksic, F. M., Jenkins, R., Joger, U., Jose, R., Kaska, Y., Kaya, U., Keogh, J. S., Köhler, G., Kuchling, G., Kumlutas, Y., Kwet, A., La Marca, E., Lamar, W., Lane, A., Lardner, B., Latta, C., Latta, G., Lau, M., Lavin, P., Lawson, D., LeBreton, M., Lehr, E., Limpus, D., Lipczynski, N., Lobo, A. S., López-Luna , M. A., Luiselli, L., Lukoschek, V., Lundberg, M., Lymberakis, P., Macey, R., Magnusson, W. E., Mahler, D. L., Malhotra, A., Mariaux, J., Maritz, B., Marques, O. A. V., Márquez, R., Martins, M., Masterson, G., Mathew, R., Mathews, N., Mayer, G., McCranie, J. R., Measey, G. J., Mendoza-Quijano, F., Menegon, M., Métrailler, S., Milton, D. A., Montgomery, C., Morato, S. A. A., Mott, T., Muñoz-Alonso, A., Murphy, J., Nguyen, T. Q., Nilson, G., Noguiera, C., Núñez, H., Orlov, N., Ota, H., Ottenwalder, Papenfuss, T., Pasachnik, S., Passos, P., Pauwels, O. S. G., Pérez-Buitrago, N., Pérez-Mellado, V., Pianka, E. R., Pleguezuelos, J., Pollock, C., Ponce-Campos, P., Powell, R., Pupin, F., Quintero Díaz, G. E., Radder, R., Ramer, J., Rasmussen, A. R., Raxworthy, C., Reynolds, R., Richman, N., Rico, E. L., Riservato, E., Rivas, G., da Rocha, P. L. B., Rödel, M. -O., Rodríguez Schettino, L., Roosenburg, W. M., Ross, J. P., Sadek, R., Sanders, K., Santos-Barrera, G., Schliech, H. H., Schmidt, B. R., Schmitz, A., Sharifi, M., Shea, G., Shi, H. -T., Shine, R., Sindaco, R., Slimani, T., Somaweera, R., Spawls, S., Stafford, P., Stuebing, R., Sweet, S., Sy, E., Temple, H. J., Tognelli, M. F., Tolley, K., Tolson, P. J., Tuniyev, B., Tuniyev, S., Üzüm, N., van Buurt, G., Van Sluys, M., Velasco, A., Vences, M., Veselý, M., Vinke, S., Vinke, T., Vogel, G., Vogrin, M., Vogt, R. C., Wearn, O. R., Werner, Y. L., Whiting, M. J., Wiewandt, T., Wilkinson, J., Wilson, B., Wren, S., Zamin, T., Zhou, K., Zug, G., and Mateo, J. A. (2013). The conservation status of the world's reptiles. *Biological Conservation*, 157:372-385.

Branton, M. and Richardson, J. S. (2011). Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. *Conservation Biology,* 25(1):9-20.

Brockway, D. G., Outcalt, K. W. and Boyer, W. D. (2007). Longleaf pine regeneration ecology and methods. In *The Longleaf Pine Ecosystem* (pp. 95-133). Springer, New York, NY.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., and Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, 16(4):909-923.

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

Cristescu, R. H., Rhodes, J., Frére, C. and Banks, P. B. (2013). Is restoring flora the same as restoring fauna? Lessons learned from koalas and mining rehabilitation. *Journal of Applied Ecology,* 50:423–431.

Cross, S. L., Bateman, P. W., and Cross, A. T. (2020). Restoration goals: why are fauna still overlooked in the process of recovering functioning ecosystems and what can be done about it?. *Ecological Management and Restoration,* 21(1):4-8.

Enge, K.M. (2001). The pitfalls of pitfall traps. *Journal of Herpetology,* 35:467-478.

Frick, K. M., Ritchie, A. L., and Krauss, S. L. (2014). Field of dreams: restitution of pollinator services in restored bird-pollinated plant populations. *Restoration Ecology,* 22:832-840.

Gibbons, J. W., Scott, D. E., Ryan, T. J., Buhlmann, K. A., Tuberville, T. D., Metts, B. S., Greene, J. L., Mills, T., Leiden, Y., Poppy, S., and Winne, C. T. (2000). The global decline of reptiles, déjà vu amphibians: reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. *BioScience*, 50(8):653-666.

Guyer, C. and Bailey, M. A. (1993). Amphibians and reptiles of longleaf pine communities. In *Proceedings of the Tall Timbers Fire Ecology Conference*, 18:139-158.

Hilderbrand, R. H., Watts, A. C., and Randle, A. M. (2005). The myths of restoration ecology. *Ecology and Society,* 10(19).

Hooke, R. L., Martín-Duque, J. F., and Pedraza, J. (2013). Land transformation by humans: a review. *GSA Today,* 22(12):4-10.

Hoss, S. K., Guyer, C., Smith, L. L. and Schuett, G. W. (2010). Multiscale influences of landscape composition and configuration on the spatial ecology of eastern diamond-backed rattlesnakes (*Crotalus adamanteus*). *Journal of Herpetology,* 44:110–123.

Howze, J. M. and Smith, L. L. (2021). The influence of prescribed fire on site selection in snakes in the longleaf pine ecosystem. *Forest Ecology and Management,* 481:118703.

Lehtinen, R. M. and Galatowitsch, S. M. (2001). Colonization of restored wetlands by amphibians in Minnesota. *American Midland Naturalist,* 145:388–396.

Mazerolle, M. J., Bailey, L. L., Kendall, W. L., Royle, J. A., Converse, S. J., and Nichols, J. D. (2007). Making great leaps forward: accounting for detectability in herpetological field studies. *Journal of Herpetology*, 41(4):672-689.

McAlpine, C., Catterall, C. P., MacNally, R., Lindenmayer, D., Reid, J. L., Holl, K. D., Bennett, A. F., Runting, R. K., Wilson, K., Hobbs, R. J., Seabrook, L., Cunningham, S., Moilanen, A., Maron, M., Shoo, L., Lunt, I., Vesk, P., Rumpff, L., Marint, T. G., Thomson, J., and Possingham, H. (2016). Integrating plant and animal-based perspectives for more effective restoration of biodiversity. *Frontiers in Ecology and the Environment,* 14:37-45.

Means, D. B. (2007). Vertebrate faunal diversity of longleaf pine ecosystems. In *The Longleaf Pine Ecosystem* (pp. 157-213). Springer, New York, NY.

Munro, N. T., Lindenmayer, D. B., and Fischer, J. (2007). Faunal response to revegetation in agricultural areas of Australia: a review. *Ecological Management and Restoration,* 8:199–207.

Nichols, O. G. and Grant, C. D. (2007). Vertebrate fauna recolonization of restored bauxite mines-Key findings from almost 30 years of monitoring and research. *Restoration Ecology,* 15:116–126.

Palmer, M. A., Ambrose, R. F., and Poff, N. L. (1997). Ecological theory and community restoration ecology. *Restoration Ecology*, 5:291-300.

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P., Fernandez-Manjarrés, J. F., Araujo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, H. D., Gilman, E. L., Guenette, S., Hurtt, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R. J., Sumaila, U. R., and Walpole, M. (2010). Scenarios for global biodiversity in the 21st century. *Science*, 330(6010):1496-1501.

Rands, M. R., Adams, W. M., Bennun, L., Butchart, S. H., Clements, A., Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J. P., Sutherland, W. J., and Vira, B. (2010). Biodiversity conservation: challenges beyond 2010. *Science*, 329(5997):1298-1303.

Ryberg, W. A., Walkup, D. K., Hibbitts, T. J., Pittman, W., Porter, V. H., Bowers, B. C., Fielder, C. M., Brown, P., Lopez, R. R., Preston, J. R., Johnson, J. T., and Hagedorn, B. W. (2021). Effective camera trap snake surveys at a rarely accessible longleaf pine savanna. *Herpetological Review,* 52(4):719-724.

Society for Ecological Restoration (International Science and Policy Working Group). (2004). The SER International Primer on Ecological Restoration. Washington, DC: Society for Ecological Restoration.

Steen, D.A. (2010). Snakes in the grass: secretive natural histories defy both conventional and progressive statistics. *Herpetological Conservation Biology,* 5:183-188.

Steen, D. A., Smith, L. L., Conner, L. M., Litt, A. R., Provencher, L., Hiers, J. K., Pokswinski, S., and Guyer, C. (2013). Reptile assemblage response to restoration of fire-suppressed longleaf pine sandhills. *Ecological Applications,* 23:148–158.

Todd, B. D., Willson, J. D., and Gibbons, J. W. (2010). 'Ecotoxicology of Amphibians and Reptiles.' (CRC Press: Boca Raton, FL.)

Tomlinson, S., Arnall, S. G., Munn, A., Bradshaw, S. D., Maloney, S. K., Dixon, K. W., and Didham, R. K. (2014). Applications and implications of ecological energetics. *Trends in Ecology and Evolution*, 29(5):280-290.

# CHAPTER 2

# ESTIMATING THE EFFECTIVENESS OF USING WILDLIFE CAMERAS VERSUS VISUAL ENCOUNTER SURVEYS TO DETECT HERPETOFAUNA[1]

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# Abstract

Efficient monitoring of herpetofauna can prove challenging to agencies and NGOs responsible for their management. Wildlife cameras have been proposed as a method to monitor herpetofauna; however, estimates of detection rates and factors impacting detection by cameras are generally lacking, therefore limiting their application. We determined the effect of body size and temperature differential on the detection of snakes and frogs by passive infrared (PIR) wildlife cameras. We hypothesized that detection would differ among models and be positively correlated with the body size and the surface temperature differential between the animal and substrate. We then conducted a field study to compare the detection of herpetofauna by a traditional method with PIR cameras. We tested 10 cameras of seven models on five snakes and one camera on six frogs. Photographs were downloaded to determine the detection rate of each species by each camera. We then chose a camera model to compare two herpetofauna survey methods: drift fences equipped with cameras and visual encounter surveys. Surveys were conducted monthly over 12 months in Irwin County, GA, USA. The highest mean detection rates of snakes were 0.65 (SE = 0.33), 0.50 (SE = 0.34), and 0.49 (SE = 0.34) for the Browning Dark Ops, Reconyx Hyperfire 2, and Mossy Oak Covert Scouting Camera, respectively. The detectability of larger snakes was greater than smaller snakes and increased as the absolute temperature differences between the snake and the substrate increased. The detectability of frogs was influenced by absolute temperature differential alone. PIR cameras generated 5 times more observations, documented more herpetofauna species, and were 7 times more efficient than traditional surveys. The effectiveness of PIR cameras to detect herpetofauna varies among models and depends on the likelihood the animal will have a significantly different body temperature than the substrate. PIR cameras generated observations far more efficiently than traditional sampling methods. PIR wildlife cameras may be most effective at detecting larger,

diurnal herpetofauna and least effective at detecting smaller, nocturnal species. Wildlife cameras have the potential to efficiently monitor some herpetofauna, providing a means to better evaluate management objectives.

## Introduction

Monitoring is an integral but often neglected component of biodiversity conservation programs (Block *et al.* 2001; Suding 2011). Monitoring is necessary to determine the efficacy of past management actions and inform future efforts (Cooke *et al.* 2019). Lack of monitoring requirements and high costs frequently constrain monitoring efforts, meaning that land managers often leave monitoring out of the restoration planning process altogether (Bash and Ryan 2002; Cross *et al.* 2019). For example, in a study of ecological restoration projects in Mexico, only 57% (n = 43 out of 75) established a monitoring plan before initiating the restoration work (Méndez-Toribio *et al.* 2021). In situations where some post-restoration monitoring is conducted, assumptions about ecosystem recovery (i.e., the Field of Dreams hypothesis) often focus exclusively on plant communities or highly mobile and easily surveyed fauna such as insects or birds (Cristescu *et al.* 2012; Cross *et al.* 2019). Surveying the same few species based on the ease of survey effort rather than monitoring a wide range of species critical to ecosystem function can negatively affect the development of restored ecosystems (Hilderbrand *et al.* 2005; Cross *et al.* 2019). The development of low-cost, efficient monitoring techniques is important to expanding monitoring efforts for a wider range of wildlife in restored ecosystems (Elphick 2008).

Herpetofauna are widely regarded as strong candidates for studying restoration success and ecosystem health (Thompson *et al.* 2008; Welsh and Hodgeson 2008), yet they are some of the least frequently studied species in restored ecosystems (Munro *et al.* 2007). This is likely due in part to the challenges associated with sampling these taxa. Common methods used to survey amphibian and reptile communities include physical capture in passive pitfall or funnel traps along drift fences or during visual searches. Both pitfall and funnel traps along drift fences require frequent checking and can result in the desiccation or predation of trapped individuals (Enge 2001). Cover boards are effective for capturing amphibians and smaller snake species, and result in fewer mortalities compared to pitfall traps; however, high temperatures at certain points of the year render cover objects unusable by some species (Kjoss and Litvaitis 2001; Halliday and Blouin-Demers 2015). Visual encounter surveys including road surveys can be less sensitive to biased detection associated with body size but often have very low detection rates (Klauber 1939; Enge and Wood 2002). Aside from cover boards, each of these methods requires significant effort during sampling periods to reduce harm or death to target and non-target species. At the same time, high-frequency or long-duration sampling is often required to generate enough detections for monitoring population responses to management. Thus, the effective use of these conventional methods for monitoring requires a high investment of time, which in turn often limits the spatial extent, replication, and temporal coverage of sampling efforts. Efficient, productive long-term survey techniques are needed to make monitoring herpetofauna populations ethical and effective.

The use of passive infrared (PIR) wildlife cameras has emerged as a method for passively conducting inventories of herpetofauna and other small-bodied wildlife (Ariefiandy *et al.* 2013; Welbourne *et al.* 2013; Neuharth *et al.* 2020; Amber *et al.* 2021; Boynton *et al.* 2021). When targeting smaller species, wildlife cameras are typically mounted on a downward-angled pole or within an inverted bucket. Deploying cameras along drift fences in place of pitfall or funnel traps can reduce labor requirements and lower the risk of animal mortality (Martin *et al.* 2017). Studies using PIR wildlife cameras to capture images of snakes have been successful in detecting primarily large, diurnal species, but appear to have failed to detect smaller-bodied or nocturnal species that one would expect are present (Amber *et al.* 2021; Boynton *et al.* 2021; Ryberg *et al.* 2021). This is likely due to the trigger system of most commonly available PIR wildlife cameras. PIR cameras rely on a combination of temperature differential and movement to trigger the camera, and small species may not create enough movement or have a body surface temperature sufficiently different from the surface environment to trigger the camera (Tobler *et al.* 2008). Notably, previous studies lack estimates of PIR camera detection rates for herpetofauna, which may lead to improper inferences of detectability based strictly on the number of photos captured in the field (Ryberg *et al.* 2021).

The main objectives of this study were to 1) estimate the detection rates of snakes by commercially available wildlife cameras, 2) to quantify the influence of body size and the surface temperature differential between the individual and substrate on the detectability of two representative groups of herpetofauna (snakes and frogs), and 3) compare the performance of the chosen PIR wildlife camera model to traditional herpetofauna survey methods. We chose to examine the relative performance of different camera models because the costs of cameras can vary substantially, models differ in features, and prior research found that PIR-triggered cameras differ in their detection rate of species and individuals over distance, temperature ranges, time of day, and numerous other factors (Driessen *et al.* 2017; Apps and McNutt 2018). We hypothesized that detection rates would differ among camera models, increase with body mass, and increase with the difference between body surface temperature and substrate surface temperature. Some PIR wildlife cameras can be programmed to take time-lapse photos or a combination of time-lapse and PIR-triggered photos. Therefore, we also examined whether using both PIR and time-lapse influenced the detectability of snakes. Finally, we compared the number of observations and species observed at drift fences equipped with PIR cameras compared to the traditional method of active visual encounter surveys including natural and artificial cover object searches.

## Methods

### *Collection sources of animals for laboratory camera system testing*

In October 2021, we opportunistically captured snakes at the Whitehall Forest in Athens, Georgia. Snakes were found using visual searches of natural and artificial cover objects including woody debris, rock crevices, and cover boards. Three wild snakes were captured for the purpose of this study: a juvenile eastern ratsnake, *Pantherophis alleghaniensis*; a red-bellied snake, *Storeria occipitomaculata*; and a southern ring-necked snake, *Diadophis punctatus.* In addition, two captive snakes were used in this study: a red cornsnake, *Pantherophis guttatus*; and an eastern kingsnake, *Lampropeltis getula.* The mass in grams and snout-to-vent length (SVL) in centimeters of each snake was recorded the day before testing began (Table 1).

In 2021, we captively reared gopher frogs (*Rana capito*) from eggs to metamorphosis in Athens, Georgia. Four of these juvenile frogs were used in this study, in addition to two captive adult gopher frogs reared in previous years. Since amphibians can experience significant fluctuations in fresh mass due to water loss (Feder and Burggren 1992), the mass in grams of each frog was recorded daily before testing began (Table 1).

### *Preparation of camera systems*

We tested cameras using the Adapted-Hunt Drift Fence Technique (AHDriFT) camera system method (Martin *et al.* 2017). This method combines components of the Camera Overhead

Augmented Temperature (COAT) and Hunt systems (Welbourne 2013; McCleery *et al.* 2014). Each of these methods surveys wildlife by funneling animals into confined spaces containing a wildlife camera. We constructed the camera housing following the methodology of Martin et al. (2017), with some modifications. Specifically, we 1) attached two continuous guides made of flexible plastic mesh near the entrance and exit of the system to direct animals under the sensor and lens of the camera and 2) fastened the cameras to a plywood board using a metal bar held in place with bolts and wing nuts, which allowed for easy exchange of cameras between trials while ensuring similar placement (Figure 1). Cameras were all set to high sensitivity and programmed to take one photo per trigger event with 30 seconds between PIR triggers.

### *Laboratory tests of wildlife cameras*

Ten cameras representing seven different models (Table 2) were tested using snakes. When available, we tested more than one unit for a given model to see how consistent a given model might be. Tests were conducted over two substrates: sand and a painted bucket lid. Sand is the natural substrate at the site where systems were eventually deployed, while a painted plastic lid was used in the original publication of this method (Martin *et al.* 2017). The same observer (AKB) conducted all tests of snakes. Each snake was tested individually. Before each trial, the surface temperature of the substrate and snake was taken with a General 10:1 Infrared Thermometer (±2 °C). The surface temperature of the snakes and substrate were not manipulated but varied naturally among trials based on the behavior of snakes while in their housing (e.g., resting under a heat lamp or in a retreat). We placed each snake at the entrance of the system a total of five times per camera. A detection occurred when the snake triggered the camera, and a non-detection occurred when the snake passed through the system but did not trigger the camera. The time it took the snake to move entirely through the system was recorded in seconds, and the snake was removed from the system if it did not voluntarily exit within three minutes. This process was repeated with each of the five snakes for each of the ten cameras over each of the two substrates for a total of 500 trials. Following the initial trials on all cameras, we used the same protocol to measure the detection rates of the three highest-performing models when the time-lapse function was used in conjunction with the PIR trigger (n = 75 trials). Cameras were programmed to take one photo per trigger event with 30 seconds of quiet time between PIR triggers, and one photo on a time-lapse with 60 seconds of quiet time between images. Photographs from each wildlife camera were downloaded to determine the number of trials in which each snake was detected.

The selection of a camera model for use in the field portion of the experiment was based on the performance of the cameras in laboratory tests and the accessibility of each camera based on price and availability. For these reasons, we decided to use the Mossy Oak Covert Scouting Camera in the field portion of this experiment. Once this model was chosen, we measured the detection rate of gopher frogs for this camera model because gopher frogs are another priority species for at our study site and across the southeastern United States. The gopher frog trials were all conducted using sand as the substrate. Tests were conducted by the observers DH, NS, JM, and AKB. Each frog was tested individually. Before each trial, the surface temperature of the substrate and frog was taken with a General 10:1 Infrared Thermometer (±2 °C). The surface temperature of the substrate was not artificially modified, but the temperature of the frogs was manipulated. Unlike the snakes, which had heat sources in their enclosures and therefore acquired a natural temperature differential from the substrate, the frogs' temperatures did not naturally differ from the substrate when removed from their housing. Therefore, to create temperature differences between frogs and substrates, we raised or lowered frog body temperatures up to 4 °C by placing them in a container that was warmed or cooled via a water bath. We then placed each frog at the entrance of the system a total of five times per trial. The time it took the frog to move entirely through the system was recorded in seconds. The frog was nudged if it did not voluntarily pass through the system within one minute. This process was repeated with each of the six frogs at least once, for a total of 72 trials. Photographs were then downloaded to determine the number of trials in which each frog was detected.

### *Field tests of wildlife cameras*

Fieldwork was conducted in Alapaha River Wildlife Management Area (ARWMA), a 2,780-hectare historic longleaf pine (*Pinus palustris*) site in Irwin County, Georgia, USA. In the mid-1960s, much of the property was converted to silviculture. Despite this, ARWMA retained small areas of historic xeric sandhill habitat with resident populations of eastern indigo snakes (*Drymarchon couperi*), gopher tortoises (*Gopherus polyphemus*), and a suite of other species.

On 1 and 2 April 2022, we deployed Mossy Oak Covert Scouting Cameras at 20 different sites across the property separated by at least 375 meters (Figure 2). Each camera was mounted directly to an inverted 18.9 L bucket, providing protection for the camera, and limiting the number of false triggers by reducing background movement. To obtain focused, clear pictures at short range, the focal length of the cameras was modified following the procedure detailed in Uhe et al. (2020). Camera settings were identical to those in the laboratory trials: 1 photo per burst with an inter-trigger interval of 30 seconds between PIR triggers. The flash on each camera was dimmed using Gorilla tape (Gorilla Glue Company, Cincinnati, OH USA) so that images taken at night would not be washed out. The camera systems were placed at the center of Y-arrayed drift fences with three 6-meter-long wings (Figure 3). To compare a traditional survey method to the camera survey method, we also deployed five artificial cover objects constructed of black tarp (122 cm x 122 cm) at each site. The cover objects were deployed within 50-m x 50-m plots that were centered around the camera arrays to ensure that the traditional and camera methods were sampling the same species assemblages. The same random pattern was used to deploy the cover objects at each site.

Between May 2022 and April 2023, each site was visited within the first 7 days of each month to service cameras and conduct a visual encounter survey. Visual encounter surveys were conducted within the 50-m x 50-m plots surrounding each camera and consisted of one person-hour spent searching natural cover (i.e., pine straw, woody debris, vegetation), artificial cover (i.e., cover objects), and scoping gopher tortoise burrows. All herpetofauna located during visual encounter surveys were identified to species level and recorded. Images from the cameras were manually processed by AKB using Camelot Project's camera trap software (Hendry & Mann 2017).

### *Data Analysis*

A set of candidate models was represented by generalized linear models (GLM) for both snake and frog detections. GLM model fitting was performed using package *stats* for R ver. 4.1.0 (R Core Team 2021). We used a binary response variable indicating detection [1] (e.g., animal passed under camera and was photographed at least once) or non-detection [0] (e.g., animal passed under camera but was not photographed). Models for snake detection included combinations of camera model, camera cost, substrate, mass, and absolute temperature differential as fixed effects. Models for frog detection included combinations of mass and absolute temperature differential as fixed effects. We used package *AICcmodavg* (Mazerolle

2017) for model selection. We did not include time-lapse in the snake detection models because we have a relatively small number of replicates with time-lapse compared to without time-lapse and those trials didn't represent the range of snake sizes and differences between body temperature and substrate temperatures. Therefore, we summarize the time-lapse trials separately and discuss any clear differences in detection rates.

For the field study, we summarized the number of herpetofauna species detected by each method for the 12-month survey period and calculated the time to conduct each sampling method and the number of observations per person hour. We then calculated three community measures for each trapping method: herpetofauna species richness, herpetofauna abundance, and observation rate (number of observations per person-hour of effort). For each of these metrics, we compared the results for the two methods for each site (*n* = 20) using a paired Student's *t*-test with the t.test function from package *stats* (R Core Team 2021).

### *Ethics Statement*

Animal care and use procedures for this study were performed according to approved University of Georgia Animal Care and Use Protocols A2021 09-017-Y1-A0, A2022 03-005-Y1-A0, A2021 02-010-Y3-A2, and A2017 02-019-Y3-A7.

## Results

### *Laboratory Test Results*

Snakes took an average of 74 seconds (range: 2-438 seconds, SD = 64.92) to pass entirely through the camera system. The surface temperature of the plastic lid averaged 20.8 °C (range: 19.9-22.1 °C, SD = 0.49). The surface temperature of the sand substrate averaged 20.8 °C (range: 18.6-25.1 °C, SD = 0.22). The surface temperature of the snakes averaged 21.8 °C (range: 19.4-

25.1 °C, SD = 1.01). The surface temperature differential between the snakes and the substrate averaged 1.1 °C (range: -1.8-4.4 °C, SD = 1.05). The camera was triggered in 204 of the 500 trials, for an overall detection rate of 40.8%.

The best model for the snake data included the camera model and the interaction mass * average temperature differential (Table 3). This model excludes two factors, substrate type and camera cost. There was very strong evidence that the probability of detection differed among camera models (Table 4). The cameras with the highest marginal predicted detection rates were the Browning Dark Ops (detection rate = 0.65, 95% CI = 0.49-0.78, SE = 0.33, n = 50), Reconyx Hyperfire 2 (0.50, 95% CI = 0.34-0.66, SE = 0.34, n = 50), and Mossy Oak Covert Scouting Camera (0.49, 95% CI = 0.33-0.65, SE = 0.34, n = 50). For the cameras where two individual cameras of the same model were tested, there did not appear to be a significant difference between camera performance within the same model (Figure 4).

There was strong evidence of an interaction between snake mass and the absolute temperature differential between the snake and substrate on detection ($\beta = 0.493$, $SE = 0.155$, $z = 3.180$, $p = 0.001$). The detectability of snakes with a mass of 16 grams or less was not influenced by the absolute temperature differential between the animal and the substrate, while, for larger snakes, detection increased significantly with the absolute temperature differential (Figure 5). The largest snake, *L. getula*, was detected most frequently (76 detections, n = 100), while the smallest snake, *S. occipitomaculata*, was detected least frequently with a (3 detections, n = 100). For the two smallest snakes, the inclusion of timelapse increased the detection rate of *S. occipitomaculata* from 0.00 to 0.33 and *D. punctatus* from 0.13 to 0.33 (Figure 6). The inclusion of timelapse did not affect the detection rate of larger snakes.

Frogs took an average of 71 seconds (range: 2-140 seconds, SD = 25.79) to pass entirely through the camera system. The surface temperature of the substrate averaged 18.2 °C (range: 13.0-20.2 °C, SD = 2.19). The surface temperature of the frogs averaged 18.5 °C (range: 10.5-24.5 °C, SD = 3.95). The surface temperature differential between the frogs and the substrate averaged 0.2 °C (range: -4-4.7 °C, SD = 2.44). The camera was triggered in 36 of the 70 trials, for an overall detection rate of 51.4%.

The best model for the frog data contained only absolute temperature differential, indicating that there was little to no evidence that mass influenced the detectability of frogs (Table 3). There was strong evidence that the absolute temperature differential between the frog and the substrate influenced detectability ($\beta = 0.795$, $SE = 0.283$, $z = 2.809$, $p = 0.005$). A frog that was the same temperature as the substrate had a ~25% chance of being detected, while a frog that was 4 degrees Celsius warmer or cooler than the substrate had a 75% chance of being detected (Figure 7).

### *Field Test Results*

We detected a minimum of 30 species of herpetofauna across all sites and survey methods including ten snakes, six lizards, two turtles, 10 frogs, and two salamanders (Table 5). We reference the minimum number of species due to some identifications being possible only to higher order identification. At least 23 species of herpetofauna were recorded by camera trapping compared with 18 species recorded by visual encounter surveys. There was very strong evidence that the species richness recorded by the camera traps at each site was greater than that recorded using visual encounter surveys ($t = 7.7122$, $df = 19$, $p = <0.001$).

We identified 13 species of herpetofauna using camera surveys that were not identified during visual encounter surveys (Table 5). This included high-priority species such as the eastern diamondback rattlesnake, Florida pine snake, and tiger salamander (*Ambystoma tigrinum*). We identified seven species of herpetofauna using visual encounter surveys that were not identified using camera surveys. This included five amphibian species and two snake species, with a notable single observation of one high-priority reptile species, the eastern indigo snake.

We recorded a total of 997 herpetofauna observations for both methods combined (Table 4). Cameras yielded 833 independent observations of herpetofauna compared to the 164 encounters yielded by the visual encounter surveys. There was very strong evidence that the total number of independent observations recorded by the camera traps at each site was greater than that recorded using visual encounter surveys ($t = 9.468$, $df = 19$, $p = <0.001$).

There was very strong evidence that the observation rate of herpetofauna by cameras was greater than visual encounter surveys ($t = 9.8162$, $df = 19$, $p = <0.001$). Deploying the camera arrays took 100 person-hours, collecting SD cards and repairing fencing took 6.8 hours, and processing images took approximately 30 hours for a total of 136.8 person-hours of work. The camera survey method, therefore, produced 6.12 observations of herpetofauna per person-hour. The visual encounter surveys took a total of 187.64 person-hours to conduct, producing 0.88 observations of herpetofauna per person-hour of work.

## Discussion

Our laboratory results were consistent with other studies of herpetofauna using PIR wildlife cameras, which found no significant difference in the number of reptile detections when a homogenous background (i.e., corkboard) was utilized as opposed to a natural substrate (Welbourne 2013, Richardson *et al.* 2018). We found that between the plastic bucket lid and sand, the type of substrate underneath the camera did not strongly influence the detection rate of snakes. Therefore, in upland sandhill habitats, cameras mounted in the inverted bucket housing can detect snakes without modification of the substrate. Conversely, we found that the body size of the snakes and the absolute surface temperature differential between the snakes and the substrate had a strong effect on detection probability. This finding is consistent with previous research on other taxa that identified body size as an essential factor in detection by cameras (Rowcliffe *et al.* 2011, Anile and Devillard 2016; Hoffmeester *et al.* 2017). Model studies of wildlife cameras have also found surface temperature differential between the subject and background to be a significant predictor of detection probability (McIntyre *et al.* 2020). In herpetofauna, reduced temperature differential of species active at night has been found to limit the effectiveness of camera traps for detecting nocturnal species (Welbourne 2013; Richardson 2014). Our study was the first to directly measure how factors such as size and surface temperature differential influenced the detection rate of snakes by wildlife cameras and to quantify the detection rate of different species based on these trends. These data indicate that wildlife cameras may prove most useful in the study of large, diurnal reptiles that are better able to maintain a temperature differential and less effective for studies of small or nocturnal species that are less likely to achieve a temperature differential great enough to trigger the PIR sensor.

The results of our tests on Gopher frogs deviated slightly from our findings with snakes. As with snakes, the absolute surface temperature differential between the frog and substrate positively affected detection (Figure 7), but detection did not differ between smaller and larger frogs. The lack of a size effect was likely the result of the small size differences among frogs compared to snakes. Though we detected a relatively high proportion of frogs when their body temperatures were several degrees different from the surface, such differences are unlikely under natural field conditions. Gopher frogs and other nocturnal amphibians are relatively poikilothermic (Brattstrom 1979) and likely to be similar in temperature to the ground surface. Therefore, our tests suggest that PIR cameras would likely be around 25% effective at detecting a frog that passes under the camera. The poor effectiveness of using PIR cameras for surveying frogs and other amphibians has been confirmed in prior studies (Pagnucco *et al.* 2011). The Hobbs Active Light Trigger (HALT) active infrared (AIR) method (Hobbs and Brehme 2017) has been proposed as a means of overcoming the difficulty of monitoring small, nocturnal herpetofauna using cameras. This method requires special integration of an AIR trigger, which is a near-infrared beam mounted parallel to an elevated threshold (Hobbs and Brehme 2017). While this method has been validated as highly effective for detecting amphibians in the laboratory and the field, the integration of an AIR trigger increases initial costs and maintenance costs and requires more substantial housing for the camera system (Hunt 2019).

Our results demonstrate that different camera models vary in their ability to detect snakes, with detection rates spanning from 20% to 60% (Figure 4). Camera model variability in detection rates has been well documented in mammals (Jacobs and Ausband, 2018; Hofmeester *et al.* 2019; McIntyre *et al.* 2020; Palencia *et al.* 2022) and our findings confirm that performance differs when surveying herpetofauna as well. In our highly controlled environment with uniform backgrounds and guides directing animals underneath the sensor and lens of the cameras, differences in detection rate between models were substantial. Therefore, when utilizing PIR wildlife cameras to study herpetofauna or other similar wildlife, it is necessary to determine the detectability of a target species by a particular camera model. The prices of wildlife cameras ranged from $40 to $1,200 USD with the average camera costing $100 to $200 (Trolliet *et al.* 2014), so cost might be considered when selecting a camera model. Our results did not suggest detection was strongly correlated with cost (Table 3), but we encourage those who plan to use wildlife cameras to monitor herpetofauna to also consider detection rates and not simply costs when selecting a camera model. Previous studies have also found significant differences in the performance among individual camera traps of the same model (Hughson *et al.* 2010; McIntyre *et al*. 2020). While we did not have the resources to test two copies of each camera model used in this experiment, those that we did display only minimal differences in detection probability (Figure 4).

Utilizing time-lapse rather than PIR sensors is one way to improve the detection of smaller or nocturnal herpetofauna or avoid differences in detection among camera models. Other studies of herpetofauna found that the PIR-trigger detected snakes on more occasions than just using the time-lapse cameras (Welbourne *et al.* 2019), but when used in conjunction, we found no effect on the detection of large snakes and a notable improvement in detecting small snakes. Therefore, if targeting small, nocturnal reptiles or amphibians, using time-lapse appears to have a reasonable detection rate. However, we caution that adding time-lapse will significantly increase post-processing time and labor, reducing the efficiency of using cameras. During our field trials using only the PIR trigger, we generated an average of 209 images per month per camera (~7 images per camera per day). In contrast, a single camera programmed to a 60-second time-lapse interval will generate 43,200 images per month (1,440 pictures per day). For our study, a one-year study using 20 PIR cameras would generate an average of ~50,000 images; but conducting the same one-year study using time-lapse would generate 10,368,000 images. We found that the monthly rate of PIR images was manageable for one person, but a 207-times increase in that number would be logistically prohibitive. With the increasing capacity of artificial intelligence (AI) to process wildlife camera images (Vélez *et al.* 2023), the capacity to process high volumes of photos might make the use of time-lapse feasible and broaden the efficacy of wildlife cameras to detect small, nocturnal herpetofauna. However, at present, we found this capacity is not available for effectively processing images in search of herpetofauna. Therefore, current choices about whether to use time-lapse, PIR, or a combination of both depends on the target species of the study and the resources and technical capacities of the investigators.

Wildlife cameras continuously collected data during our entire 12-month survey period, and because of this, they captured more species and observations than the traditional survey method. The wildlife cameras recorded five more species and five times as many individual encounters of herpetofauna as traditional visual encounter surveys. While the cameras consistently outperformed visual searches in detecting reptiles, both methods detected few amphibian species. Our low numbers of amphibians detected on cameras may reflect a low abundance of amphibians in the terrestrial areas we monitored. Previous studies have had success at detecting some amphibian species using wildlife cameras (Martin *et al.* 2017; Amber *et al.* 2021); however, our laboratory study suggests that at least some part of the low detection of amphibians in the field was due to the relatively low detection rate of amphibians by PIR cameras. Additionally, it is likely that the behavioral traits and movement patterns of certain species could lead to a lack of detection. The modified AHDriFT design is most likely to be biased against detections of arboreal, aquatic, and fossorial species and towards detections of fast-moving, terrestrial snake and small vertebrate species.

Achieving the goals of habitat restoration requires monitoring faunal responses. Wildlife cameras provide a more efficient and productive means for monitoring a range of herpetofauna compared to many standard approaches. As an alternative to traditional pitfall or funnel trap monitoring methods, PIR, time-lapse, or AIR cameras have the potential to reliably monitor snakes and other herpetofauna while reducing bycatch of non-target species and preventing short or long-term harm to animals (Greenberg *et al.* 1994; Enge 2001, Hobbs and Brehme 2017, Hunt 2019, this study). When conducting a community-level study on species that vary in size and activity patterns, preliminary work must be conducted to determine how species-specific characteristics such as body size and environmental factors will affect detection (Stokeld *et al.* 2015; Apps and McNutt 2018). For example, laboratory estimates of size-specific detection rates could be used to inform detection rates in occupancy or abundance analyses (e.g., informed priors of detection). We assert that PIR wildlife cameras are particularly suitable for detecting large, diurnal herpetofauna. It is unclear yet whether PIR cameras are adequate for detecting amphibians, and they appear poorly suited to detecting small, nocturnal snakes. Targeting these types of species may require the use of time-lapse, though image processing may limit this potential. Alternatively, AIR triggers might be needed to sufficiently detect small, nocturnal species. Despite these potential setbacks, using cameras at our restoration site was significantly more productive for surveying herpetofauna than traditional visual encounter surveys using cover objects. This method has strong potential to reduce barriers to implementing long-term monitoring projects aiming to study herpetofauna and other small wildlife species.

# Literature Cited

Amber ED, Lipps GJ, Peterman WE (2021) Evaluation of the AHDriFT camera trap system to survey for small mammals and herpetofauna. *Journal of Fish and Wildlife Management* **12**, 197–207.

Anile S, Devillard S (2016) Study design and body mass influence RAIs from camera trap studies: evidence from the Felidae. *Animal Conservation* **19**, 35–45.

Apps P, McNutt JW (2018) Are camera traps fit for purpose? A rigorous, reproducible and realistic test of camera trap performance. *African Journal of Ecology* **56**, 710–720.

Ariefiandy A, Purwandana D, Seno A, Ciofi C, Jessop TS (2013) Can camera traps monitor Komodo dragons a large ectothermic predator?. *PLoS One* **8**, e58800.

Bash JS, Ryan CM (2002) Stream restoration and enhancement projects: Is anyone monitoring?. *Environmental Management* **29(6)**, 877-885.

Block WM, Franklin, AB, Ward, JP Jr, Ganey JL, White GC (2001) Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restoration Ecology* **9**, 293-303.

Boynton MK, Toenies M, Cornelius N, Rich LN (2021) Comparing camera traps and visual encounter surveys for monitoring small animals. *California Fish and Wildlife* **107(2),** 99-117.

Brattstrom BH (1979) Amphibian temperature regulation studies in the field and laboratory. *American Zoologist* **19(1)**, 345-356.

Cooke SJ, Bennett JR, Jones, HP (2019) We have a long way to go if we want to realize the promise of the "Decade on Ecosystem Restoration". *Conservation Science and Practice* **1**, e129.

Cristescu RH, Frère C, Banks PB (2012) A review of fauna in mine rehabilitation in Australia: current state and future directions. *Biological Conservation* **149(1)**, 60-72.

Cross SL, Tomlinson S, Craig MD, Dixon KW, Bateman PW (2019) Overlooked and undervalued: the neglected role of fauna and a global bias in ecological restoration assessments. *Pacific Conservation Biology* **25(4)**, 331-341.

Driessen MM, Jarman PJ, Troy S, Callander S (2017) Animal detections vary among commonly used camera trap models. *Wildlife Research* **44(4),** 291-297.

Elphick CS (2008) How you count counts: the importance of methods research in applied ecology. *Journal of Applied Ecology* **45(5)**, 1313-1320.

Enge KM (2001) The pitfalls of pitfall traps. *Journal of Herpetology* **35**, 467-478.

Enge KM, Wood KN (2002) A pedestrian road survey of an upland snake community in Florida. *Southeastern Naturalist* **1(4)**, 365-380.

Feder ME, Burggren WW (Eds.) (1992). 'Environmental Physiology of the Amphibians.' (University of Chicago Press: Chicago, IL, USA)

Greenberg CH, Neary DG, Harris LD (1994) A comparison of herpetofaunal sampling effectiveness of pitfall, single-ended, and double-ended funnel traps used with drift fences. *Journal of Herpetology* **28(3)**, 319-324.

Halliday W, Blouin-Demers G (2015) Efficacy of coverboards for sampling small northern snakes. *Herpetology Notes* **8**, 309-314.

Hendry H, Mann C (2017) Camelot–intuitive software for camera trap data management. *BioRxiv* **203216**.

Hilderbrand RH, Watts AC, Randle AM (2005) The myths of restoration ecology. *Ecology and Society,* **10(19).**

Hobbs MT, Brehme CS (2017) An improved camera trap for amphibians, reptiles, smal mammals, and large invertebrates. *PloS one* ***12*****(10),** e0185026.

Hofmeester TR, Cromsigt JP, Odden J, Andrén H, Kindberg J, Linnell JD (2019) Framing pictures: a conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecology and Evolution* **9(4)**, 2320-2336.

Hughson DL, Darby NW, Dungan JD (2010) Comparison of motion-activated cameras for wildlife investigations. *California Fish and Game* **96**, 101-109.

Hunt JD (2019) Improving monitoring and habitat assessment for gopher frog (*Rana capito*) management in Georgia. MS thesis (University of Georgia: Athens, GA, USA)

Jacobs CE, Ausband DE (2018) An evaluation of camera trap performance–What are we missing and does deployment height matter? *Remote Sensing in Ecology and Conservation* **4(4)**, 352-360.

Kjoss VA, Litvaitis JA (2001) Comparison of two methods to sample snake communities in early successional habitats. *Wildlife Society Bulletin*, 153-157.

Klauber LM (1939) Studies of reptile life in the arid southwest, Part I. Night collecting in the desert with ecological statistics. *Bulletin of the Zoological Society of San Diego* **14**, 2-64.

Martin SA, Rautsaw RM, Robb F, Bolt MR, Parkinson CL, Seigel RA (2017) Set AHDriFT: applying game cameras to drift fences for surveying herpetofauna and small mammals. *Wildlife Society Bulletin* **41(4)**, 804-809.

Mazerolle MJ (2017) Package 'AICcmodavg'. *R package* **281**.

McCleery RA, Zweig CL, Desa MA, Hunt R, Kitchens WM, Percival HF (2014) A novel method for camera-trapping small mammals. *Wildlife Society Bulletin* **38(4),** 887-891.

McIntyre T, Majelantle TL, Slip DJ, Harcourt RG (2020) Quantifying imperfect camera-trap detection probabilities: implications for density modelling. *Wildlife Research* **47(2)**, 177-185.

Méndez-Toribio M, Martínez-Garza C, Ceccon E (2021) Challenges during the execution, results, and monitoring phases of ecological restoration: Learning from a country-wide assessment. *PloS one* **16(4)**, e0249573.

Munro NT, Lindenmayer DB, Fischer J (2007) Faunal response to revegetation in agricultural areas of Australia: a review. *Ecological Management and Restoration* **8**, 199–207.

Neuharth DB, Ryberg WA, Adams CS, Hibbitts TJ, Walkup DK, Frizzell SL, Johnson TE, Pierce BL, Pierce JB, Rudolph DC (2020) Searching for rare and secretive snakes: are camera-trap and box-trap methods interchangeable? *Wildlife Research* **47(6)**, 476-484.

Palencia P, Vicente J, Soriguer RC, Acevedo P (2022) Towards a best-practices guide for camera trapping: assessing differences among camera trap models and settings under field conditions. *Journal of Zoology* **316(3)**, 197-208.

Pagnucco KS, Paszkowski CA, Scrimgeour GJ (2011) Using cameras to monitor tunnel use by long-toed salamanders (*Ambystoma macrodactylum*): an informative, cost-efficient technique. *Herpetological Conservation and Biology* **6(2),** 277–86.

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Richardson E (2014) A comparison of passive infrared automatically triggered cameras with pitfall traps as methods for surveying reptiles in semi-arid ecosystems. Honours (La Trobe University, Melbourne, VIC, Australia).

Richardson E, Nimmo DG, Avitabile S, Tworkowski L, Watson SJ, Welbourne D, Leonard SW (2018) Camera traps and pitfalls: an evaluation of two methods for surveying reptiles in a semiarid ecosystem. *Wildlife Research* **44(8)**, 637-647.

Rowcliffe JM, Carbone C, Jansen PA, Kays R, Kranstauber B (2011) Quantifying the sensitivity of camera traps: an adapted distance sampling approach. *Methods in Ecology and Evolution* **2**, 464–476.

Ryberg WA, Walkup DK, Hibbits TJ, Pittman W, Porter VH, Bowers BC, Fielder CM, Brown P, Lopez RR, Preston JR, Johnson JT, Hagedorn BW (2021) Effective camera trap snake surveys at a rarely accessible longleaf pine savanna. *Herpetological Review* **52(4)**, 719-724.

Stokeld D, Frank AS, Hill B, Choy JL, Mahney T, Stevens A, Young S, Rangers D, Rangers W, Gillespie GR (2015) Multiple cameras required to reliably detect feral cats in northern

Australian tropical savanna: an evaluation of sampling design when using camera traps. *Wildlife Research* **42**, 642–649.

Suding KN (2011) Toward an era of restoration in ecology: Successes, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics* **42**, 465-487.

Thompson SA, Thompson GG, Withers PC (2008) Rehabilitation index for evaluating restoration of terrestrial ecosystems using the reptile assemblage as the bio-indicator. *Ecological Indicators* ***8*****(5),** 530-549.

Tobler MW, Carrillo-Percastegui SE, Leite Pitman R, Mares R, Powell G (2008) An evaluation of camera traps for inventorying large-and medium-sized terrestrial rainforest mammals. *Animal Conservation* **11(3)**, 169-178.

Trolliet F, Vermeulen C, Huynen MC, Hambuckers A (2014) Use of camera traps for wildlife studies: a review. *Biotechnologie, Agronomie, Société et Environnement* **18(3).**

Uhe L, Albrecht K, Schleicher A, Engler JO (2020) Adjusting trail cameras to improve monitoring of small open cup nesting birds. *Journal of Ornithology* **161(3),** 893-899.

Vélez J, McShea W, Shamon H, Castiblanco-Camacho PJ, Tabak MA, Chalmers C, Fergus P, Fieberg J (2023) An evaluation of platforms for processing camera-trap data using artificial intelligence. *Methods in Ecology and Evolution* **14(2)**, 459-477.

Welbourne DA (2013) A method for surveying diurnal terrestrial reptiles with passive infrared automatically triggered cameras. *Herpetological Review* **44**, 247–250.

Welbourne DJ, Claridge AW, Paull DJ, Ford F (2019) Improving terrestrial squamate surveys with camera-trap programming and hardware modifications. *Animals* **9(6),** 388.

Welsh HH, Hodgson GR (2008) Amphibians as metrics of critical biological thresholds in forested headwater streams of the Pacific Northwest, U.S.A. *Freshwater Biology* **53**, 1470–1488.

Table 2.1. Snout to vent length (SVL; in centimeters) of snakes and masses (in grams) of snakes and frogs used to test camera traps.

| Group | Species | SVL (cm) | Mass (g) |
|---|---|---|---|
| Snakes | *Diadophis punctatus* | 25.5 | 6.5 |
| | *Lampropeltis getula* | 100.3 | 470.0 |
| | *Pantherophis alleghaniensis* | 41.5 | 16.0 |
| | *Pantherophis guttatus* | 140.0 | 783.0 |
| | *Storeria occipitomaculata* | 10.7 | 2.8 |
| Frogs | *Rana capito,* A1 | NA | 53.5-59.7 |
| | *Rana capito,* A2 | NA | 64.3-70.2 |
| | *Rana capito,* J1A | NA | 13.0 |
| | *Rana capito,* J1B | NA | 12.8 |
| | *Rana capito*, J6A | NA | 10.8 |
| | *Rana capito*, J6B | NA | 10.0 |

Table 2.2. Models of wildlife cameras compared for survey deployment using the Adapted-Hunt Drift Fence Technique (AHDriFT) camera system method.

| Manufacturer | Camera | Model | Approximate Cost, $USD |
|---|---|---|---:|
| Browning | Dark Ops | BTC-6PXD | 350 |
| Browning | Recon Force HP4 | BTC-7E-HP4 | 190 |
| Mossy Oak | Covert Scouting Camera (x2) | Hollywood | 150 |
| Moultrie | M80 GameSpy Digital Camera (x2) | MFH-DGS-M80 | 150 |
| Reconyx | Hyperfire 2 | HP2W Professional | 460 |
| Reconyx | Hyperfire 2 | HP2X Professional | 460 |
| Stealth Cam | G30 Infrared Scouting Cam (x2) | STC-G30 | 77 |

Table 2.3 Model selection using generalized linear models (GLM) for factors influencing detectability of snakes and frogs. K, number of parameters; AICc, Akaike Information Criterion; atd, absolute temperature differential.

| Group | Model | K | AICc | ΔAICc |
|---|---|---|---|---|
| Snake | mass*atd + camera | 13 | 536.92 | 0.00 |
| | mass*atd + camera + substrate | 14 | 537.69 | 0.77 |
| | mass*atd + cost | 5 | 541.98 | 5.06 |
| | mass*atd + cost + substrate | 6 | 542.69 | 5.77 |
| | mass + atd + camera + substrate | 13 | 547.00 | 10.08 |
| | mass*atd | 4 | 552.52 | 15.60 |
| | mass + atd | 3 | 567.44 | 30.52 |
| | mass | 2 | 576.69 | 39.77 |
| | atd | 2 | 637.06 | 101.06 |
| Frog | atd | 2 | 91.91 | 0.00 |
| | mass + atd | 3 | 93.12 | 1.21 |
| | mass*atd | 4 | 95.18 | 3.27 |
| | mass | 2 | 100.68 | 8.77 |

Table 2.4. Results of the generalized linear model (GLM) of variables influencing the detection rate of snakes. ATD, absolute temperature differential. Significance codes: * < 0.05, ** < 0.01, *** <0.001

| Coefficient | Estimate | Standard error | Z value | P value | |
|---|---|---|---|---|---|
| Intercept | 0.598 | 0.328 | 1.826 | 0.068 | |
| Mass | 0.974 | 0.121 | 8.032 | <0.001 | *** |
| ATD | 0.385 | 0.127 | 3.032 | 0.002 | ** |
| Mass:ATD | 0.493 | 0.155 | 3.180 | 0.001 | ** |
| Browning Recon | -1.194 | 0.468 | -2.555 | 0.011 | * |
| Mossy Oak A | -0.628 | 0.463 | -1.356 | 0.174 | |
| Mossy Oak B | -1.083 | 0.468 | -2.317 | 0.021 | * |
| Moultrie A | -1.446 | 0.471 | -3.070 | 0.002 | ** |
| Moultrie B | -1.413 | 0.496 | -2.849 | 0.004 | ** |
| Reconyx HP2X | -1.234 | 0.480 | -2.572 | 0.010 | * |
| Reconyx HP2W | -0.591 | 0.462 | -1.280 | 0.201 | |
| Stealth Cam A | -2.052 | 0.504 | -4.074 | <0.001 | *** |
| Stealth Cam B | -2.285 | 0.519 | -4.402 | <0.001 | *** |

Table 2.5. The number of independent observations of herpetofauna species made via camera or visual encounter surveys in Alapaha River WMA, Irwin County, GA, USA over 12 months.

| Group | Scientific name | Common name | # Observations | |
|---|---|---|---|---|
| | | | Drift fence/ camera | VES/cover object |
| Reptiles | *Coluber constrictor* | black racer | 189 | 4 |
| | *Crotalus adamanteus* | eastern diamondback rattlesnake | 4 | 0 |
| | *Diadophis punctatus* | southern ring-necked snake | 0 | 1 |
| | *Drymarchon couperi* | eastern indigo snake | 0 | 1 |
| | *Heterodon platirhinos* | eastern hognose snake | 19 | 0 |
| | *Masticophis flagellum* | coachwhip | 38 | 1 |
| | *Nerodia erythrogaster* | common water snake | 1 | 0 |
| | *Pantherophis alleghaniensis* | eastern rat snake | 7 | 0 |
| | *Pantherophis guttatus* | red corn snake | 2 | 0 |
| | *Pituophis melanoleucus* | Florida pine snake | 1 | 0 |
| | *Anolis carolinensis* | green anole | 75 | 26 |
| | *Aspidoscelis sexlineatus* | six-lined racerunner | 178 | 3 |
| | *Plestiodon egregius* | mole skink | 4 | 0 |
| | *Plestiodon laticeps* | broadhead skink | 13 | 2 |
| | *Plestiodon* spp. | skink species | 36 | 1 |
| | *Sceloporus undulatus* | eastern fence lizard | 224 | 40 |
| | *Scincella lateralis* | ground skink | 25 | 53 |
| | *Gopherus polyphemus* | gopher tortoise | 2 | 19 |
| | *Terrapene carolina* | eastern box turtle | 1 | 2 |
| Amphibians | *Ambystoma tigrinum* | tiger salamander | 1 | 0 |
| | *Eurycea quadridigitata* | southeastern dwarf salamander | 0 | 1 |
| | *Acris gryllus* | southern cricket frog | 0 | 2 |
| | *Anaxyrus quercicus* | oak toad | 1 | 1 |
| | *Anaxyrus terrestris* | southern toad | 2 | 0 |
| | *Gastrophryne carolinensis* | eastern narrow-mouthed toad | 0 | 1 |
| | *Hyla femoralis* | pine woods treefrog | 0 | 2 |
| | *Lithobates catesbeiana* | bullfrog | 1 | 0 |
| | *Lithobates sphenocephalus* | southern leopard frog | 1 | 0 |
| | *Pseudacris crucifer* | spring peeper | 1 | 0 |
| | *Pseudophilautus ocularis* | little grass frog | 0 | 4 |
| | *Scaphiopus holbrookii* | eastern spadefoot toad | 7 | 0 |
| Total | | | 833 | 164 |

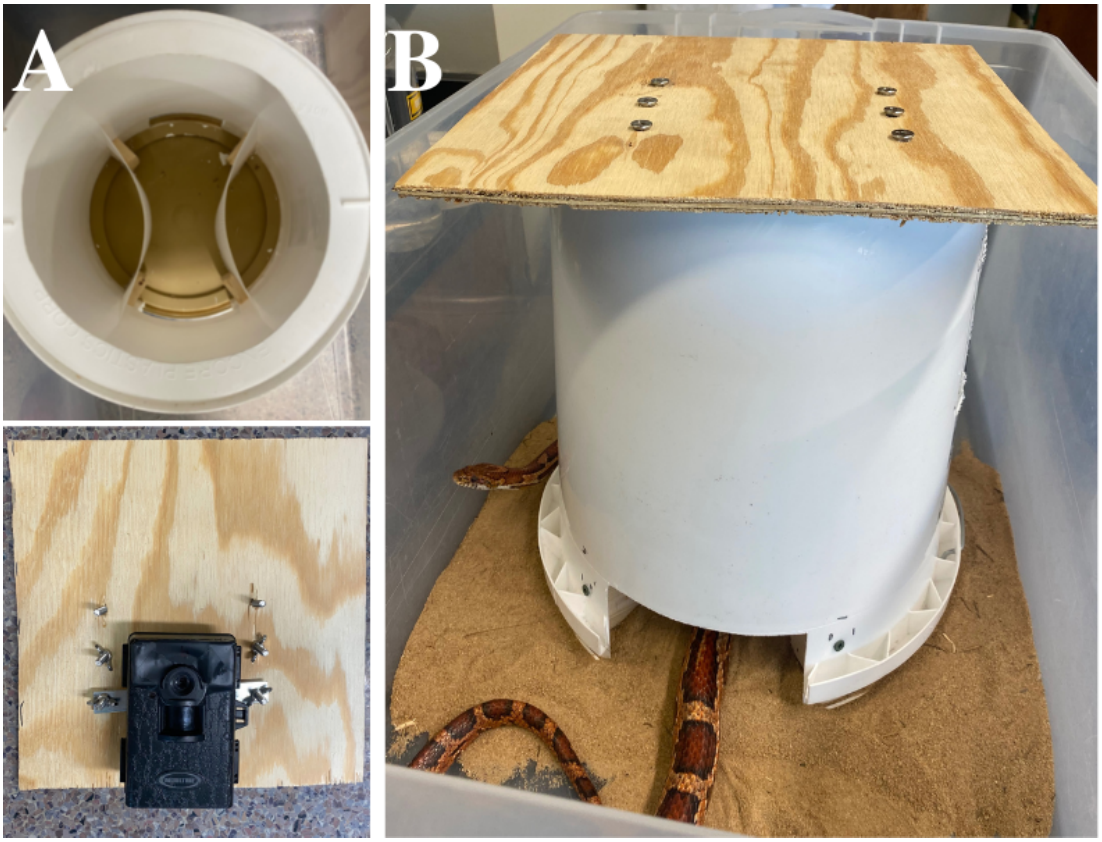

Figure 2.1. Adapted-Hunt Drift Fence Technique (AHDriFT) camera system. (A) Interior of camera housing system and (B) Fully assembled housing during a trial on *Pantherophis guttatus*.

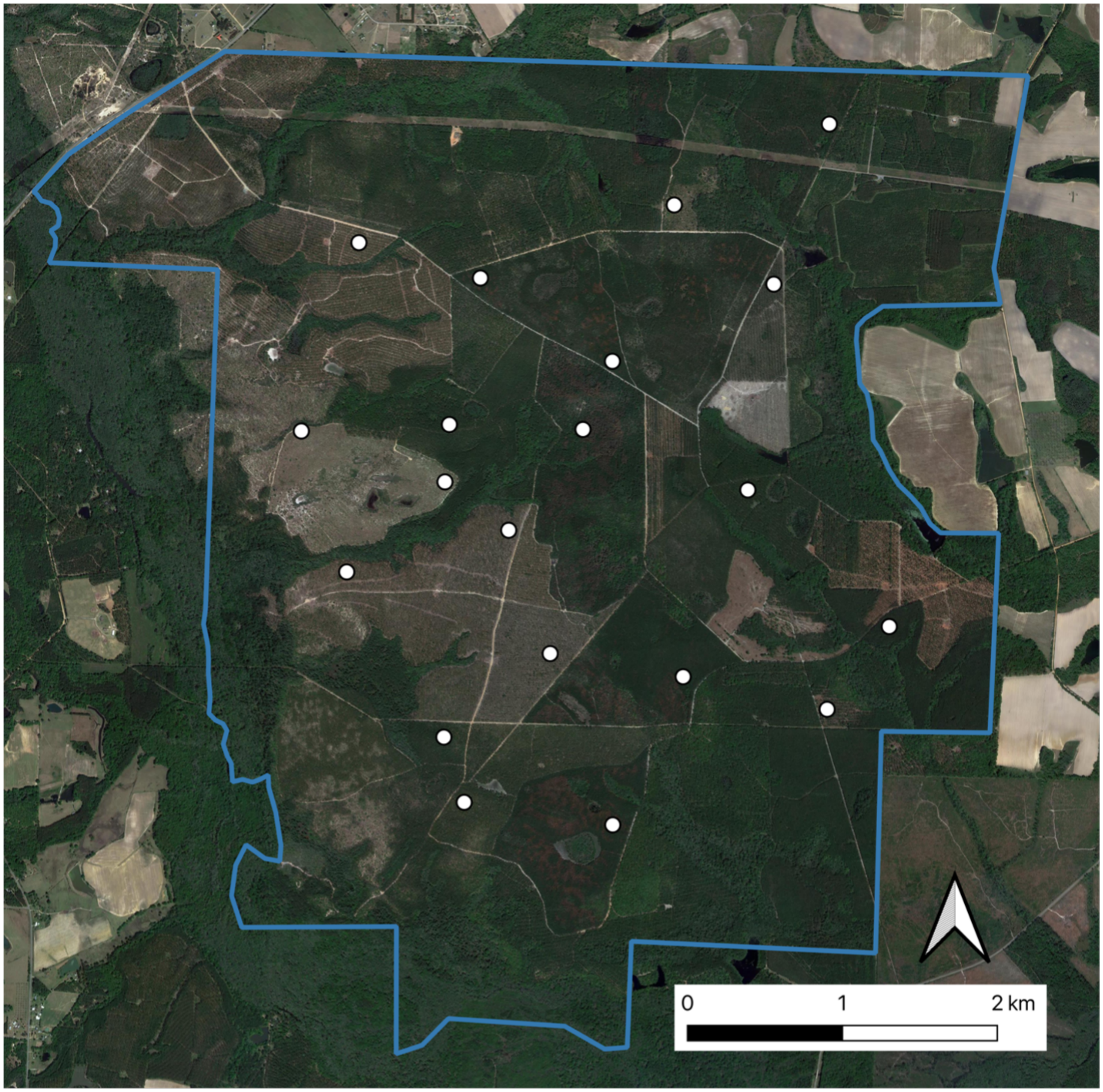

Figure 2.2. Aerial image with the location of 20 sites within Alapaha River Wildlife Management Area, Iwrin County, GA, USA.

Figure 2.3. Modified AHDriFT system with Y-shaped drift fence array deployed at Alapaha River Wildlife Management Area, Irwin County, GA, USA.

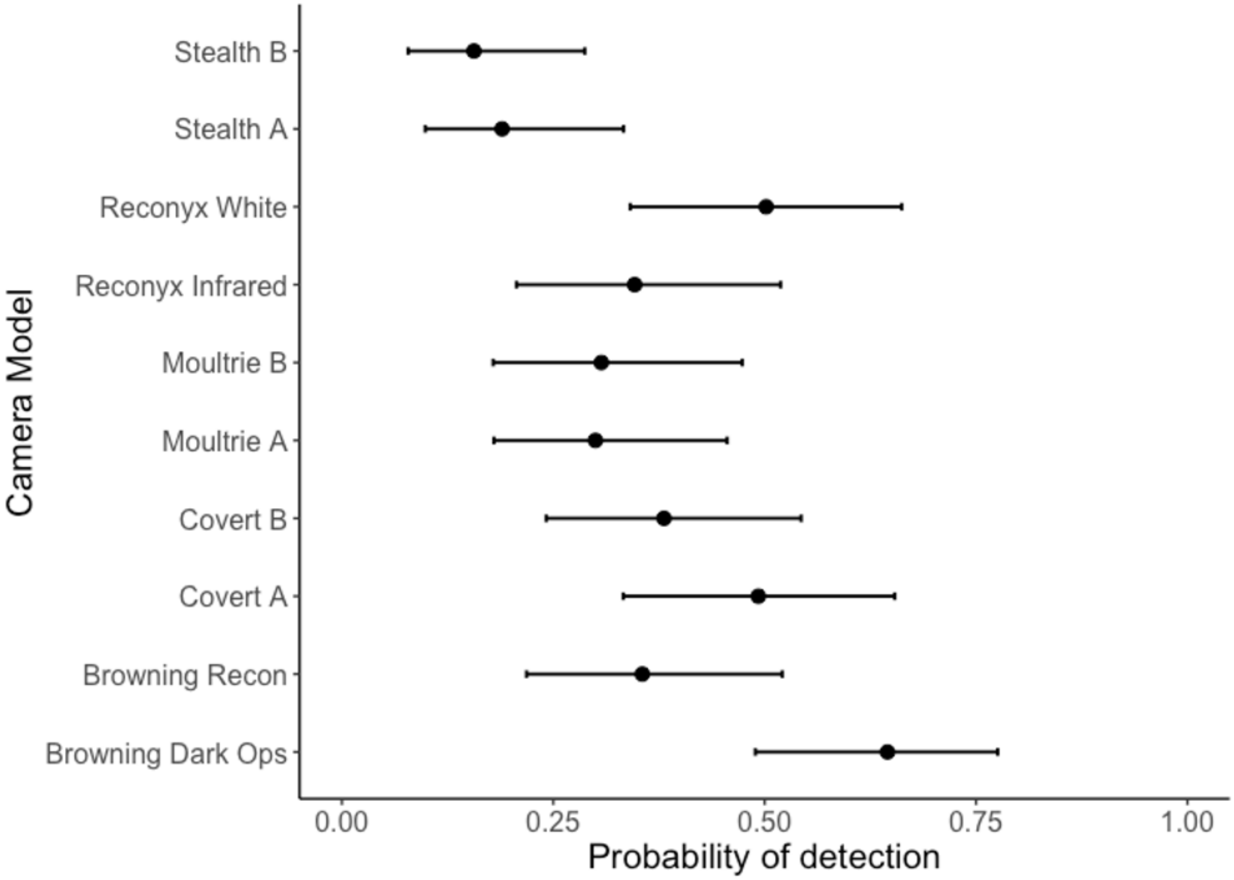

Figure 2.4. Marginal predicted detection rate and 95% CI of each camera tested on snakes.

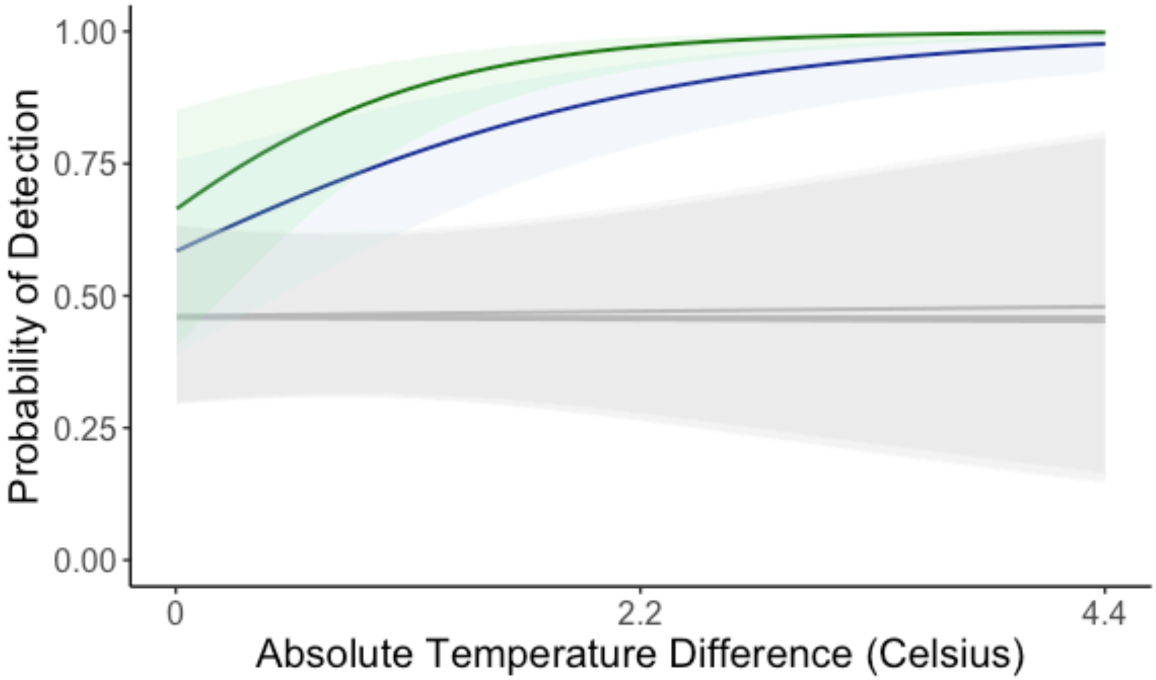

Figure 2.5. Marginal predicted effects of the absolute temperature differential between the animal and the substrate temperature for snake species of different body sizes across all camera models ($\beta = 0.493$, $SE = 0.155$, $z = 3.180$, $p = 0.001$). The green line represents *Pantherophis guttatus* and the blue line represents *Lampropeltis getula*.

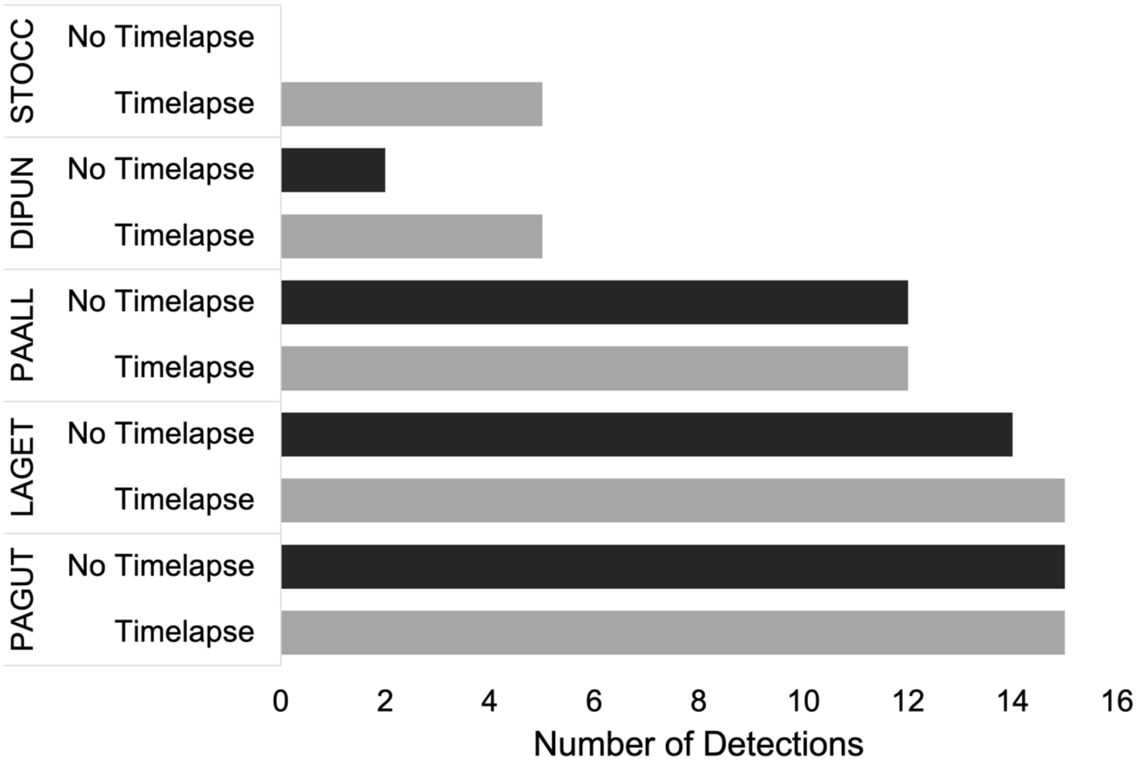

Figure 2.6. Detection rate for the following snake species with and without the use of time-lapse using three camera models (Browning Dark Ops, n = 5; Recoynx Hyperfire 2, n = 5; and Mossy Oak Covert Scouting Camera, n = 5): *Storeria occipitomaculata* (STOCC), *Diadophis punctatus* (DIPUN), *Pantherophis alleghaniensis* (PAALL), *Lampropeltis getula* (LAGET), and *Pantherophis guttatus* (PAGUT).

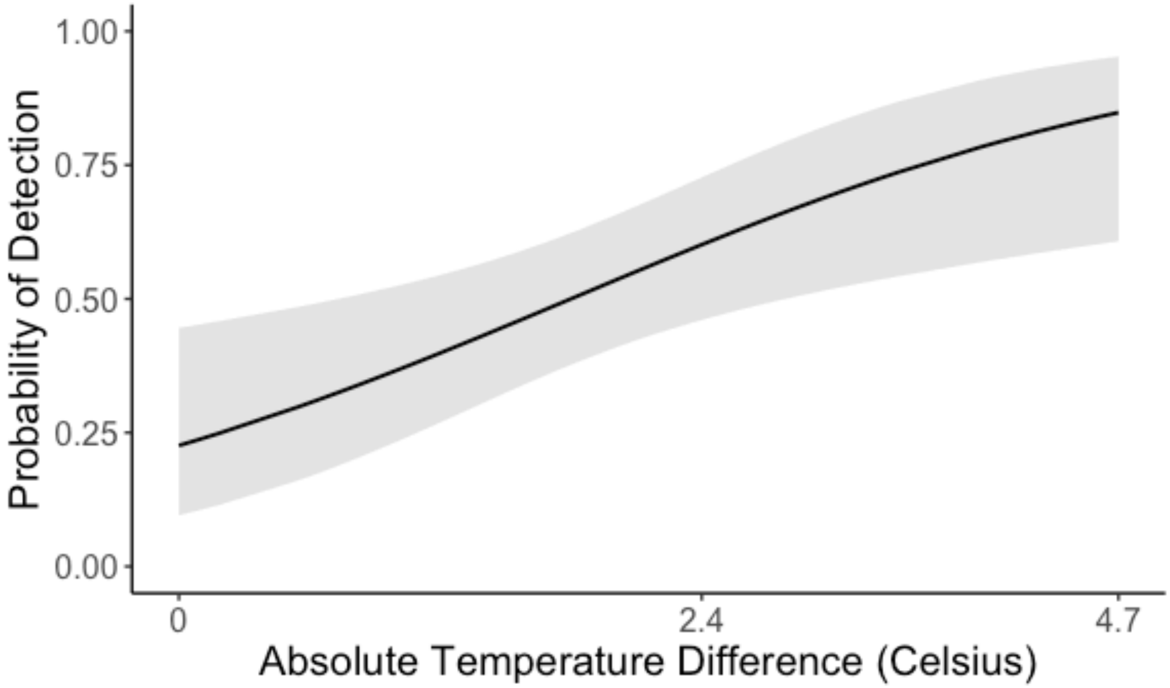

Figure 2.7. Marginal predicted effect of absolute temperature differential between the animal and the substrate on detection of *Rana capito* during laboratory trials ($\beta = 0.795$, *SE* = 0.283, $z = 2.809$, $p = 0.005$).

# CHAPTER 3

# MEASURING SQUAMATE PATCH OCCUPANCY IN A PUBLICLY MANAGED LANDSCAPE UNDERGOING RESTORATION[2]

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[2] Brown, A. K. and Maerz, J. C. 2023. To be submitted to *Ecological Applications*.

# Abstract

While habitat restoration is a foundational approach in conservation, care must be taken to determine when habitat restoration alone might prove insufficient for species recovery in restored areas. This is relevant to the Alapaha River Wildlife Management Area (ARWMA), a historic longleaf pine (*Pinus palustris*) site that was converted to intensive pine forestry more than 60 years ago and is now being aggressively restored. Although ARWMA is regularly surveyed for listed species including Eastern indigo snakes (*Drymarchon couperi*) and Gopher tortoises (*Gopherus polyphemus*), a site-wide survey to determine the effectiveness of restoration efforts for other reptile species has not been conducted. This study aims to estimate whether current restoration efforts are improving near-term site occupancy for a suite of non-target or secondary-target fauna, specifically squamates (snake and lizard species). We predicted that occupancy of squamates will increase with declining pine basal area but will also be dependent on the length of time since primary restoration (thinning and high frequency prescribed fire) and negatively correlated with distance from potential remnant source habitats. We used one year of wildlife camera data in a Bayesian hierarchical community occupancy model to estimate squamate occupancy for multiple species as a function of pine basal area, years since primary restoration, and distance from remnant habitat. There was a positive relationship between years since thinning and a negative relationship between years since burning and squamate occupancy, though these estimated relationships appeared relatively small, had a high uncertainty, and varied among species. The results of this study and long-term monitoring will inform the prioritization of sites for restoration and decisions about corridors or assisted migration to facilitate the dispersal of species to restored sites.

# Introduction

The field of restoration ecology emerged in response to anthropogenic land use change as a method of "assisting the recovery of ecosystems that have been damaged, degraded, or destroyed" (Society for Ecological Restoration 2004). While ecological restoration has the potential to increase the amount of available habitat, there are implicit assumptions associated with attempting to recreate a system that formed over the course of millennia in a matter of months, years, or even decades. The failure to recognize and address these assumptions (i.e., myths about the ability to create exact copies of historic ecosystems by recreating plant communities, utilization of standardized methods in inappropriate situations, etc.) can lead to unsatisfactory results (Hilderbrand et al. 2005). The Field of Dreams Hypothesis (Palmer et al. 1997) is one such assumption that shapes many restoration projects. This hypothesis posits that animals independently recolonize restored areas following the re-establishment of vegetation, returning to pre-disturbance population and community dynamics (Frick et al. 2004, McAlpine et al. 2016). While seemingly ubiquitous throughout restoration practice, this hypothesis has not been extensively tested and fails to acknowledge the many complex plant-animal interactions critical to ecosystem function and biogeographic constraints that affect what species under what contexts are likely to recolonize restored habitats (Cross et al. 2019, Tomlinson et al. 2014). More work is needed to understand the effectiveness of vegetation-based restoration for organisms and ecosystems targeted by these initiatives.

Several factors likely determine whether fauna respond to habitat restoration. One is external biogeographic processes such as the extent of isolation of restored habitats from potential source populations (Lehtinen and Galatowitsch 2001). A second factor is the extent to which restoration and ongoing management recreate essential conditions that support some species (Nichols and Grant 2007). For example, snake species such as the federally petitioned eastern diamondback rattlesnake (*Crotalus adamanteus*) can be affected by specific disturbance regimes (Hoss et al. 2010, Howze and Smith 2021) and the presence of keystone species that provide habitat features that allow individuals to survive and populations to persist in the face of natural disturbances and variable weather conditions. Third is the extent to which legacies of historic land use affect the performance of species within restored areas (e.g., Burrow et al. 2021). Effective restoration and conservation require evaluating the relative importance of extrinsic biogeographic and intrinsic habitat factors that limit the recovery of animal species within restored habitats. Upon evaluating these factors, land managers may ultimately have to identify additional actions such as assisted migration to complement habitat management on restored sites (Cristescu et al. 2013).

Studies of faunal responses to ecological restoration are desperately needed to determine the efficacy of restoration methods in assisting the recovery of ecosystems. Only 34 of 301 (11%) scientific articles on restoration outcomes published through November 2012 measured vertebrate diversity and abundance (Wortley et al. 2013). Much of the peer-reviewed literature assessing faunal responses to restoration has occurred in mining restoration contexts, yet only 41% of studies in restored mine sites assessed restoration outcomes for fauna (Cross et al. 2019). A review of 166 studies assessing the effects of forest restoration in agricultural, forested, and mined contexts found that abundance and diversity were studied less frequently among vertebrates than among vegetation and invertebrates (Meli et al. 2017). Vertebrate abundance and diversity response variables were reported in only 15% and 22% of studies, respectively, while 62% of studies reported on vegetation abundance and 50% reported on vegetation diversity (Meli et al. 2017). These deficiencies in monitoring programs can be detrimental to restoration projects, making it difficult to quantify the success of past actions or improve future restoration efforts (Lindenmayer 2020).

Pine savanna restoration has become a major conservation focus across the southeastern United States. Pine savannas such as the longleaf pine (*Pinus palustris*) ecosystem historically covered vast swaths of the southeastern United States. The less than 3% of old-growth longleaf pine habitat remaining now exists as relatively small, isolated "islands" supporting high levels of endemic biodiversity separated by "oceans" of developed land unsuitable for many native species (Brockway et al. 2007). While pine savanna restoration efforts have restored nearly 1 million hectares of longleaf pine habitat (United States Department of Agriculture, Natural Resources Conservation Service 2023), these projects focus primarily on plant community restoration with targeted goals for select fauna such as the Gopher tortoise (*Gopherus polyphemus*) and Red-cockaded woodpecker (*Picoides borealis*). It is believed that habitat restoration for these umbrella species will benefit other flora and fauna (Branton and Richardson 2011); however, these species often require assisted migration to colonize restored sites and the responses of additional taxa are rarely monitored and therefore remain uncertain. Therefore, as is the case in many restored ecosystems, there is a general lack of knowledge about how most fauna respond to pine savanna restoration efforts.

Several snake species that are strongly associated with pine savannas (i.e., Eastern indigo snake, *Drymarchon couperi*; Eastern diamondback rattlesnake; Florida pine snake, *Pituophis melanoleucus mugitus*; Southern hognose snake, *Heterodon simus*) are among the most threatened snake species in the southeastern United States (Todd and Andrews 2008). Isolation by distance or dispersal barriers may result in persistently low snake occupancy rates within restored habitats, especially for species that are not the direct targets of restoration (Waldron *et* *al.* 2013). This problem is exacerbated by difficulties in detecting these species (but see Brown et al.). Despite this, restoration monitoring efforts rarely measure the responses of snakes or other reptile species to management actions (Munro et al. 2007, Todd et al. 2010). Consequently, there is a lack of robust information about snake responses to habitat restoration and management, which can impede conservation efforts for these species (Gibbons et al. 2000).

Hierarchical, multi-species occupancy models can utilize detection/non-detection data, such as from wildlife cameras, to increase the precision of occupancy estimates for infrequently observed species by using correlations among species using wider community data (Zipkin et al. 2009). Unlike many snake species, many lizard species in the southeastern United States tend to be relatively abundant and readily detectable (Adams et al. 2017), and their inclusion in studies could help inform snake occupancy estimates. To better understand the effect of longleaf pine restoration on non-target reptile fauna, we used passive infrared (PIR) wildlife cameras to collect occupancy data and estimate patterns of squamate occupancy and richness in a publicly managed, pine savanna landscape undergoing restoration. Specifically, we estimated occupancy rates for various squamate species as functions of pine basal area, distance from remnant habitat, and primary time since restoration. We expected that occupancy of squamate species would increase with declining pine basal area, would be positively correlated with time since restoration, and would be negatively correlated with distance to potential source habitats.

## Methods

### *Study Area*

Alapaha River Wildlife Management Area (ARWMA) is a 2,780-hectare historic longleaf pine site in Irwin County, Georgia, USA. This property was managed for longleaf pine turpentine production until it was converted to slash pine (*Pinus elliottii*) silviculture and associated recreational uses in the mid-1960s (Georgia Department of Natural Resources 2018). Despite this, the property retained small areas of xeric sandhill habitat with resident populations of Eastern indigo snakes, Florida pine snakes, Eastern diamondback rattlesnakes, and a suite of other species. The site also retained a relatively dense Gopher tortoise population that varies among stands relative to soil conditions and forest management.

Georgia DNR purchased ARWMA in 2016 and has been aggressively restoring longleaf pine habitats across the property since 2018, thereby creating a mosaic of unrestored and restored forest patches. The restoration goals for this site focus on increasing habitat for Gopher tortoises, and targets include thinning longleaf pine stands to a basal area of 50-70 square feet per acre (11.5-16.1 square meters per hectare) and burning sites at a 1–3-year interval. When this study commenced, approximately 1,375 hectares had been thinned or clearcut, with plans for clearcuts to be reforested with longleaf pine within two years of harvest (Georgia Department of Natural Resources 2018). Since the property is bordered by the Alapaha River on two sides and a highway and agricultural fields on the other two sides, it is extremely unlikely that individuals recolonized the site from areas outside of ARWMA.

### *Data Collection*

We identified 2 historic remnants, 13 restored, and five unrestored forest "patches" across ARWMA where we conducted surveys (Figure 3.1). We characterized the restoration state of each non-remnant site based on whether its pine basal area met the DNR's stated goal of 50-70 square feet per acre (Georgia Department of Natural Resources 2018) as measured in February 2022 (Table 3.1). The remnant habitat in ARWMA, a sandhill on the western edge of the property, was never successfully converted to forestry or converted for other uses because of the xeric, nutrient-poor soils.

We determined the pine basal area of each patch by measuring the diameter at breast height of all trees in a 1/10-acre area centered around the midpoint for each study plot (i.e., “patch”) within a forest stand. We then used this value to estimate the pine basal area in square feet per acre. Pine basal area in “unrestored” patches averaged 123.04 square feet per acre (range: 81.75-167.82, SD = 31.84). Pine basal area in “restored” patches averaged 49.11 square feet per acre (range: 23.28-70.00, SD = 13.57). Pine basal area in “remnant” patches averaged 6.67 square feet per acre (range: 5.57-7.78, SD = 1.57). We used management plans provided by GADNR to determine the time since burning and thinning of forest stands across the property. The shortest, straight-line distance to the nearest remnant habitat was measured in meters using QGIS and the coordinates of the midpoint for each study plot. Distance between “unrestored” and “remnant” patches averaged 2,096 meters (range:1,200-3,310, SD = 937.94). Distance between “restored” and “remnant” patches averaged 1,463 meters (range: 175-2,935, SD = 883.5).

For this study, we used the Adapted-Hunt Drift Fence Technique (AHDriFT) camera system method (Martin *et al.* 2017; Brown, Chapter 2). This method combines components of the Camera Overhead Augmented Temperature (COAT) and Hunt systems (Welbourne 2013; McCleery *et al.* 2014). Each of these methods surveys wildlife by funneling animals into confined spaces containing a wildlife camera. We constructed the camera housing following the methodology of Martin et al. (2017), with some modifications. Specifically, we 1) attached two continuous guides made of flexible plastic mesh near the entrance and exit of the system to direct animals under the sensor and lens of the camera, 2) did not attach guides to the exterior of the bucket, and 3) fastened the cameras directly to the base of the bucket. To obtain focused, clear pictures at short range, the focal length of the cameras was modified following the procedure detailed in Uhe et al. (2020). Additionally, the flash on each camera was dimmed using gorilla tape so that images taken at night would not be washed out. Cameras were set to take 1 photo per burst with an inter-trigger interval of 30 seconds between PIR triggers.

On 1 and 2 April 2022, we deployed a Mossy Oak Covert Scouting Cameras at the center of Y-arrayed drift fences with three 20-foot-long wings at each of the 20 patches described above (Figure 3.2). Between May 2022 and April 2023, each site was visited within the first 7 days of each month to collect SD cards and repair drift fencing.

*Data Analysis*

Images from the cameras were manually processed by AKB using Camelot Project's wildlife camera software (Hendry and Mann 2017). We used a Bayesian hierarchical community occupancy model (Dorazio and Royle 2005, Homyack et al. 2017, Guzy et al. 2019) modified from Guzy et al. (2019) to estimate species-specific squamate occupancy and detection probabilities and the influence of site characteristics on snake occupancy probability and richness as a function of site-specific covariates (pine basal area, distance from remnant habitat, time since last burn, and time since thinning). By incorporating species-specific covariate effects into the modeling framework, we can estimate species-specific occupancy probabilities, site-specific species richness, and account for imperfect detection (Dorazio and Royle 2005, Zipkin et al. 2009). These species-specific parameter estimates can be considered in a community context and therefore are more precise, particularly for rare species such as the focal snakes in this study (Sauer and Link 2002, Zipkin et al. 2009, Pacifici et al. 2014). We generated species-specific, monthly observance matrices for 12 consecutive months at each site, with detection represented as 1 and non-detection as 0. The true occupancy status was denoted by $z_{ij}$ such that if species $i$ occupies site $j$ $z_{ij} = 1$, otherwise $z_{ij} = 0$. We considered the occupancy state to be a Bernoulli random variable, $z_{i,j} \sim \text{Bern}(\Psi_{i,j})$, where $\Psi_{i,j}$ is the probability that species *i* occupies site *j*. We considered species detection to be a Bernoulli random variable, $y_{i,j,k} \sim \text{Bern}(p_{i,j,k} * z_{i,j})$, where $p_{i,j,k}$ is the probability that species *i* is detected at site *j* during survey *k*. $y_{i,j,k}$ is 1 if species *i* is detected at site *j* during survey *k*, or 0 otherwise.

We modeled species-specific occupancy probability ($\Psi_{i,j}$) following a linear-logit function of the model covariates:

$$\text{logit}(\Psi_{i,j}) = \alpha_{0i} + \alpha_{1i} * \text{Distance}_j + \alpha_{2i} * \text{BasalArea}_j + \alpha_{3i} * \text{Burn}_j + \alpha_{4i} * \text{Thin}_j$$

We defined the distance covariate as the distance in meters between the center of each site and the nearest edge of the remnant “natural” habitat that was not converted to intensive forestry. We defined the basal area covariate as the pine basal area of each site in square feet per acre, as measured in February 2022. We defined the burn and thin covariates as the year in which the site was last exposed to prescribed fire or intensive logging. In a few cases, the site was burned or logged during the study. Since in most cases the camera was removed after the disturbance occurred, we retained the original thinning and prescribed burn dates for analysis. Each of the covariates was centered and scaled (i.e., [value – mean]/SD).

We also modeled species-specific detection probabilities following a linear-logit function of the model covariates:

$$\text{logit}(p_{i,j,k}) = \beta_{0i} + \beta_{1i} * \text{Size}_i + \beta_{2i} * \text{Temp}_k$$

We defined the size covariate as the average snout-to-vent length (SVL) of each species. We defined the temperature covariate as the average monthly temperature for each survey period. This covariate acts as a proxy for availability for detection, as activity patterns and captures can be influenced by the time of year sampling is conducted (Todd *et al.* 2007; Leiden *et al.* 1999).

Borrowing information to increase the precision of estimates for data-poor species is appropriate only if the species have a degree of relatedness (Pacifici et al. 2014). To ensure a degree of relatedness among species, we divided the 15 squamate species into two groups: 1) “lizards” and 2) snakes. We then drew species-specific effects from group normal distributions e.g., $\alpha_{p,\,i} \sim \text{Normal}\ (\mu_{p,h},\ \sigma^2_{p,\,h})$ for parameter $\alpha_p$ of species $i$ in group $h$, where the mean and variance are group-level hyper-parameters. We provided group mean parameters with a prior that followed a logistic distribution with a mean of 0 and a precision of 1. We provided group standard deviation parameters with a prior that followed a Uniform (0.1,3) distribution.

We fit the model using JAGS (Plummer 2003) called from R (4.1.0, R Core Team 2018) with the jags function from package *R2jags* (Su and Yajima 2015). We implemented this model in a Bayesian framework using Markov Chain Monte Carlo (MCMC) sampling to generate samples from the posterior distribution (Lunn et al. 2000). We used three Markov chains with a length of 20,000. We removed the first 2,500 as burn-in and thinned the remainder by a factor of 10. This provided 5,250 samples to approximate posterior summary statistics for each model parameter including the mean and 2.5% and 97.5% percentiles of the distribution, which represent 95% Bayesian credible intervals. We assessed model convergence via the Gelman-Rubin diagnostic and a visual inspection of chains from a subset of outputs. For each of the modeled parameters, the Gelman-Rubin statistic value was at or below 1.02 (Gelman and Rubin 1992). This outcome along with a visual inspection of the chains indicated model convergence.

## Results

The wildlife cameras were triggered 47,412 times across 12 months among the 20 patches. The images captured 816 independent observations of squamates including 555 independent observations of lizards consisting of at least six species and 261 independent observations of snakes consisting of nine species (Table 3.2). Notable species included two of the four snake species identified as species of greatest conservation need in Georgia's State Wildlife Action Plan (SWAP): the Eastern diamondback rattlesnake and Florida pine snake (Table 3.2). We also encountered a juvenile Eastern indigo snake along a drift fence, but that species was not detected in any photos. The most frequently detected snake species was the Black racer (*Coluber constrictor*) which was detected at 19 patches (naive occupancy rate = 0.95). Six snake species were detected at 2-10 patches (naive occupancy rates = 0.10-0.50), while the Plain-bellied water snake (*Nerodia erythrogaster*) and Florida pine snake were detected only once each at a single patch. Several lizard species were detected at 18 patches, including the Green anole (*Anolis carolinensis*; naive occupancy rate = 0.90), Six-lined racerunner (*Aspidoscelis sexlineata*; 0.90), and Eastern fence lizard (*Sceloporus undulatus*; 0.90). The three remaining lizard species (Broad-headed skink, *Plestiodon laticeps*; Mole skink, *Plestiodon egregious*; Ground skink, *Scincilla lateralis*) were detected at 3-13 patches (naive occupancy rates = 0.15-0.65). Skinks unidentifiable to species were detected at 6 patches and were pooled in our analyses as *Plestiodon* spp.

The mean estimated squamate species richness at each site was 11 (9-13). There was weak evidence of a negative relationship between mean estimated occupancy probability across all squamate species and distance to remnant habitat and years since the last burn (Table 3.3, Figure 3.3). For both lizards and snakes, the 95% credible intervals for the estimated slope of occupancy as a function of distance to remnant habitat overlapped zero. At the group level, each of these relationships was ambiguous, as the 95% credible intervals overlapped 0 in all estimates. However, there was a probability of 85% that the relationship between distance to remnant habitat and snake occupancy was negative and a probability of 88.6% that the relationship between time since restoration and snake occupancy was negative. There were no clear relationships between any of the covariates and mean lizard occupancy (Table 3.3).

Visually, it appeared that there were different relationships with each covariate at the species level. However, due to the high uncertainty surrounding each estimated relationship, we cannot state whether these relationships were truly different among species. Based on a visual inspection of the mean estimated occupancy probabilities and the Bayesian p-values generated from each covariate, some species appeared to respond similarly to management actions while others appeared to respond very differently. For example, the estimated occupancy probability of Eastern hognose snake (*Heterodon platirhinos*) was positively correlated with increased time since the stand was restored in 94.6% of posterior samples (Table 3.4). This pattern appeared similar for several species including the Coachwhip (*Masticophis flagellum*), Black racer, Florida pine snake, and Red corn snake (*Pantherophis guttatus*), with the estimated slope of this relationship negative in 81-94% of posterior samples (Table 3.4, Figure 3.5).

There appeared to be a negative relationship between the mean estimated occupancy probability and distance from remnant longleaf pine habitat for several snake species, but only for Coachwhips did the 95% credible intervals fail to overlap 0 (Table 3.4). The Eastern hognose snake, Red corn snake, and Plain-bellied water snake displayed a negative relationship between the mean estimated occupancy probability and distance from remnant longleaf pine habitat in greater than 81-86% of posterior samples (Table 3.4, Figure 3.4).

Only one snake and two lizards appeared to have a strong response to the pine basal area of a stand based on visual inspection of the model outputs, however these responses occurred in opposite directions. Increased pine basal area was negatively correlated with the mean estimated occupancy probability for Eastern hognose snakes with a probability of 86.8% (Table 3.4, Figure

3.7). Conversely, the pooled skink species and Ground skinks appeared to have a strong positive response to higher pine basal area, as mean estimated occupancy probability had a positive relationship with pine basal area in 82-85% of posterior estimates (Table 3.4, Figure 3.7). Only one species, the Coachwhip, appeared to respond strongly to time since the last burn occurred (Table 3.4, Figure 3.6). In 81% of posterior estimates, mean estimated occupancy of Coachwhips decreased as time since the last burn occurred increased (Table 3.4).

## Discussion

Our objective was to evaluate whether current restoration efforts are improving site occupancy – in the near term – for squamate species at ARWMA. Our results demonstrate that as a group, snake occupancy at patches within ARWMA may be positively correlated with proximity to remnant patches of longleaf pine savanna and time since restoration was implemented. Lizard occupancy did not appear to be strongly related to any of the habitat covariates measured. We documented what might be substantial variation in species responses to restoration actions at ARWMA, but we could not conclusively determine whether species responses were different because of high uncertainty in most estimates among many species. The inference we can draw about similarities or differences among species depends on the criteria used to evaluate similarities or differences in species responses (e.g., the direction of slopes, whether credible intervals overlap zero, or probability of slope overlap between species). In the context of hypothesis testing, many species had relationships to covariates with credible intervals that overlapped zero and would therefore fail conventions regarding “statistical significance”. However, from a management perspective, there were many species where non-zero estimated relationships to covariates exceeded 70% or 80% probability, so concluding that those species were not affected by distance to remnant habitat or management actions is not advised. We saw little to no evidence management actions were having negative effects on the occupancy of many species. Therefore, we believe that – in the near term – the evidence suggests that management actions to restore pine savanna conditions on ARWMA range from positive to benign for squamate species and warrant continuation.

Herpetofauna are a notoriously difficult group of taxa to study, and the combination of passive monitoring and estimation using a hierarchical Bayesian community occupancy model has the potential to improve our ability to manage these species. The passive monitoring design significantly reduced the effort required to monitor a wide suite of taxa including priority species while generating significantly more observations than traditional methods (Brown, chapter 2). The model's hierarchical nature allowed species-specific information to be borrowed from a broader, related taxonomic group, such that species-level estimates were a combination of a single-species estimate and the average parameter estimates of the group (Guzy et al. 2019). This method allows estimates to be made about species that are detected infrequently and would otherwise be inestimable (Sauer and Link 2002). Despite cameras being deployed for a full 12 months, occupancy and detection probability were extremely low for some species, which would have influenced the precision and accuracy of a single-species occupancy model (Guillera-Arroita et al. 2010). We argue that consideration of hierarchical multi-species occupancy or abundance models when designing monitoring programs can lead to more precise and efficient monitoring of the recovery of threatened and data-limited species such as herpetofauna.

Our results indicated that there was a weakly negative relationship between the mean estimated occupancy probability and distance to remnant habitat across all squamate species (Figure 3.3). This relationship appeared to be driven largely by snakes, as lizards as a group were not strongly affected by the restoration actions occurring within ARWMA (Table 3.2). Our results indicate that the response of squamates to pine savanna restoration activities may be species dependent. In alignment with other studies of herpetofauna responses to the reintroduction of fire and restoration in other ecosystems (Singh et al. 2002, Perry et al. 2009), we found that some species appeared to be positively affected by restoration efforts, others may be negatively affected, but most species did not show any clear relationship. These results support findings that certain herpetofauna affiliated with pine savanna habitats were differentially affected by recent restoration efforts (Howze and Smith 2021). Landowners should, therefore, take caution when inferring the effectiveness of restoration actions on one species' recovery based on the response of another species, even if they are taxonomically similar.

As a group, snake occupancy decreased slightly as the distance from the remnant habitat increased (Table 3.2). This potentially indicates the gradual dispersal of organisms from within the remnant habitat to surrounding areas that have since been restored. The remnant habitat in ARWMA is a sandhill on the western edge of the property. This sandhill was never successfully converted to forestry or converted for other uses because of the xeric, nutrient-poor soils. It acted as a refuge for Gopher tortoises and, consequently, a refuge for many longleaf pine affiliated snake species that persist within the property today (pers. comms.). This result demonstrates the potential importance of creating connected systems of habitat over isolated patches to increase the chance of reptile colonization and persistence in restored habitats. This may also indicate that restoration of unoccupied habitats that are too far from remnant occupied sites to be colonized naturally will require reintroductions of some species as a component of restoration efforts.

While the response to the time since thinning occurred was highly variable among species, the mean estimated occupancy probability was higher in later posttreatment stands for both snakes as a group and several snake species (Table 3.2; Table 3.3). Previous research has found that reptile communities within restored patches became indistinguishable from the community at remnant patches after extended posttreatment periods (Steen *et al.* 2013). There is an inevitable time lag between when restoration actions occur and when species not already present in the restored area will eventually recolonize it. As seen in our study, for some species, it can take years or decades before the restoration actions increase the occupancy of an area. This information is important to land managers because the time required to see increases in occupancy could exceed the extent of the monitoring project, which could lead to the devaluation of effective restoration measures. For actions such as tree thinning that change the entire structure of an ecosystem, meaningful improvements in the occupancy of fauna could become apparent only decades after thinning has occurred and assuming the restored habitat is maintained. When combined with the effect of isolation on the occupancy of restored areas, a restored site that is isolated from remnant habitat could have a protracted period between restoration and recovery of fauna, particularly for dispersal limited species.

Longleaf pine ecosystems have been shaped by frequent fires for thousands of years, and the changes resulting from fire suppression may lead to declines in some herpetofauna (Guyer and Bailey 1993). For the only one species, the Coachwhip, was there was a notable negative relationship between occupancy and increased time since the last prescribed fire. However, there were no species for which increased time since the last prescribed fire was positively associated with an increase in mean estimated occupancy probability (Table 3.3). This finding supports the continued implementation of a high-frequency (1-3 year) prescribed fire regime to best support both Gopher tortoises and other herpetofauna utilizing the pine savanna habitat at ARWMA.

While we saw little evidence management actions were having negative effects on the occupancy of many species, there were also many species that displayed minimal or no response to restoration efforts (Table 3.3). As discussed above, this could be an indication that the time since restoration is not yet long enough to positively influence the occupancy of some species. Additionally, this result could support the implementation of groundcover restoration and/or targeted invasive species removal to create suitable habitats for some fauna. Assisted migration of some dispersal limited species may also be necessary if the restored area is isolated from remnant habitats, although the appropriateness of this method for herpetofauna is widely debated due to the high mortality rates of translocated individuals relative to residents (Germano and Bishop 2009; Lee and Park 2011; Sullivan *et al.* 2015) and the need to often use soft-release strategies such as penning translocated animals (Tuberville et al. 2008).

One source of uncertainty associated with our hierarchical multispecies model relates to the “group effect” that allows information to be borrowed across species (e.g., snakes, lizards). Although the species in these two larger groups are taxonomically related, some species have different habitat requirements and life histories that may make them functionally more like a species in the other group. For example, an Eastern fence lizard utilizes forests that differ in structure from those utilized by a Six-lined racerunner (Howze and Smith 2022), while Racerunners and Coachwhips are both found mainly in xeric, sandy environments (Howze and Smith 2015) despite being in different taxonomic groups. While we chose groupings based on taxonomic groupings following the methods of Guzy *et al.* (2019), researchers could group species on any number of characteristics. Future modeling efforts aimed at informing land management could base groupings on factors relevant to the species of interest (i.e., functional diversity, size, ecological niche, diet, conservation status, etc.).

Some of our model estimates would have been improved had we not lost several of our monitoring arrays during this experiment. For example, one of the cameras was destroyed in

September 2022. This camera had previously detected two of the four Eastern diamondback rattlesnakes recorded during our study and may have provided more observations of this and other data-limited species if it remained operational to April 2023 as planned. The loss of this and several other cameras due to prescribed fire and flooding may have caused us to miss detecting some of the rarer species observed during the study period and therefore affected our model estimates. To increase the feasibility of utilizing the AHDriFT method on publicly managed landscapes, we strongly encourage the development of fire-proof camera housing. We also recommend using hardware cloth or metal sheathing in place of silt fencing for the drift fences. Finally, we strongly encourage good communication with local land managers to limit the loss of monitoring infrastructure during restoration.

The results of this study can help inform the prioritization of patches for restoration and determine whether current restoration practices are sufficient to support squamate species. Our results demonstrate that the occupancy of snakes will likely increase as time progresses given remnant longleaf pine habitat is protected and a frequent fire regime is maintained. However, the response of squamates to restoration actions and the temporal scale at which these responses became evident appeared to be highly species dependent. Therefore, decisions regarding future restoration actions should consider all species that management aims to create suitable habitats for. While restoration actions specifically for Gopher tortoises may not equally benefit all squamates species, we did not identify any concerning relationships between restoration practices on ARWMA and squamate occupancy. We urge land managers to utilize passive monitoring of fauna and multi-species occupancy models to determine whether assisted migration programs or the creation of corridors to facilitate dispersal may be needed to complement wildlife recovery on restored sites.

## Literature Cited

Adams, C. S., Ryberg, W. A., Hibbitts, T. J., Pierce, B. L., Pierce, J. B., and Rudolph, D. C. (2017). Evaluating effectiveness and cost of time-lapse triggered camera trapping techniques to detect terrestrial squamate diversity. *Herpetological Review, 48*(1):44-8.

Branton, M., and Richardson, J. S. Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. *Conservation Biology* **25(1)**, 9-20 (2011).

Böhm, M., Collen, B., Baillie, J. E., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffman, M., Livingstone, S. R., Ram, M., Rhodin, A. G. J., Stuart, S. N., van Dijk, P. P., Young, B. E., Afuang, L. E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., Akarsu, F., Alencar, L. R. V., Allison, A., Ananjeva, N., Anderson, S., Andrén, C., Ariano- Sánchez, D., Arredondo, J. C., Auliya, M., Austin, C. C., Avci, A., Baker, P. J., Barreto-Lima, A. F., Barrio-Amorós, C. L., Basu, D., Bates, M. F., Batistella, A., Bauer, A., Bennett, D., Böhme, W., Broadley, D., Brown, R., Burgess, J., Captain, A., Carreira, S., Castañeda, M. R., Castro, F., Catenazzi, A., Cedeño-Vázquez, J. R., Chapple, D. G., Cheylan, M., Cisneros-Heredia, D. F., Cogalniceanu, D., Cogger, H., Corti, C., Costa, G. C., Couper, P. J., Courtney, T., Crnobrnja-Isailovic, J., Crochet, P. -A., Crother, B., Cruz, F., Daltry, J. C., Daniels, R. J. R., Das, I., de Silva, A., Diesmos, A. C., Dirksen, L., Doan, T. M., Dodd Jr., C. K., Doody, J. S., Dorcas, M. E., Duarte de Barros Filho, J., Egan, V. T., El Mouden, E. H., Embert, D., Espinoza, R. E., Fallabrino, A., Feng, X., Feng, Z. -J., Fitzgerald, L., Flores-Villela, O., França, F. G. R., Frost, D., Gadsden, H., Gamble, T., Ganesh, S. R., Garcia, M. A., García-Pérez, J. E., Gatus, J., Gaulke, M., Geniez, P., Georges, A., Gerlach, J., Goldberg, S., Gonzalez, J. -C. T., Gower, D. J., Grant, T., Greenbaum, E., Grieco, C., Guo, P., Hamilton, A. M., Hare, K., Hedges, S. B., Heideman, N., Hilton-Taylor, C., Hitchmough, R., Hollingsworth, B., Hutchinson, M., Ineich, I., Iverson, J., Jaksic, F. M., Jenkins, R., Joger, U., Jose, R., Kaska, Y., Kaya, U., Keogh, J. S., Köhler, G., Kuchling, G., Kumlutas, Y., Kwet, A., La Marca, E., Lamar, W., Lane, A., Lardner, B., Latta, C., Latta, G., Lau, M., Lavin, P., Lawson, D., LeBreton, M., Lehr, E., Limpus, D., Lipczynski, N., Lobo, A. S., López-Luna , M. A., Luiselli, L., Lukoschek, V., Lundberg, M., Lymberakis, P., Macey, R., Magnusson, W. E., Mahler, D. L., Malhotra, A., Mariaux, J., Maritz, B., Marques, O. A. V., Márquez, R., Martins, M., Masterson, G., Mathew, R., Mathews, N., Mayer, G., McCranie, J. R., Measey, G. J., Mendoza-Quijano, F., Menegon, M., Métrailler, S., Milton, D. A., Montgomery, C., Morato, S. A. A., Mott, T., Muñoz-Alonso, A., Murphy, J., Nguyen, T. Q., Nilson, G., Noguiera, C., Núñez, H., Orlov, N., Ota, H., Ottenwalder, Papenfuss, T., Pasachnik, S., Passos, P., Pauwels, O. S. G., Pérez-Buitrago, N., Pérez-Mellado, V., Pianka, E. R., Pleguezuelos, J., Pollock, C., Ponce-Campos, P., Powell, R., Pupin, F., Quintero Díaz, G. E., Radder, R., Ramer, J., Rasmussen, A. R., Raxworthy, C., Reynolds, R., Richman, N., Rico, E. L., Riservato, E., Rivas, G., da Rocha, P. L. B., Rödel, M. -O., Rodríguez Schettino, L., Roosenburg, W. M., Ross, J. P., Sadek, R., Sanders, K., Santos-Barrera, G., Schliech, H. H., Schmidt, B. R., Schmitz, A., Sharifi, M., Shea, G., Shi, H. -T., Shine, R., Sindaco, R., Slimani, T., Somaweera, R., Spawls, S., Stafford, P., Stuebing, R., Sweet, S., Sy, E., Temple, H. J., Tognelli, M. F., Tolley, K., Tolson, P. J., Tuniyev, B., Tuniyev, S., Üzüm, N., van Buurt, G., Van Sluys, M., Velasco, A., Vences, M., Veselý, M., Vinke, S., Vinke, T., Vogel, G., Vogrin, M., Vogt, R. C., Wearn, O. R., Werner, Y. L., Whiting, M.

J., Wiewandt, T., Wilkinson, J., Wilson, B., Wren, S., Zamin, T., Zhou, K., Zug, G., and Mateo, J. A. (2013). The conservation status of the world's reptiles. *Biological Conservation*, 157:372-385.

Brockway, D. G., Outcalt, K. W. and Boyer, W. D. (2007). Longleaf pine regeneration ecology and methods. In *The Longleaf Pine Ecosystem* (pp. 95-133). Springer, New York, NY.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., and Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, 16(4):909-923.

Brown, A. B. and Maerz, J. C. Estimating the effectiveness and source of bias for using wildlife cameras to detect snakes. Masters Thesis in preparation. (Unpublished).

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

Cristescu, R. H., Rhodes, J., Frére, C. and Banks, P. B. (2013). Is restoring flora the same as restoring fauna? Lessons learned from koalas and mining rehabilitation. *Journal of Applied Ecology,* 50:423–431.

Cross, S. L., Bateman, P. W., and Cross, A. T. (2020). Restoration goals: why are fauna still overlooked in the process of recovering functioning ecosystems and what can be done about it?. *Ecological Management and Restoration,* 21(1):4-8.

Dorazio, R. M., and Royle, J. A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, 100:389-398.

Frick, K. M., Ritchie, A. L., and Krauss, S. L. (2014). Field of dreams: restitution of pollinator services in restored bird-pollinated plant populations. *Restoration Ecology,* 22:832-840.

Gelman, A. and Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science,* 7:457-472.

Georgia Department of Natural Resources. (2018). *Alapaha River Wildlife Management Area Irwin County: ten-year plan July 1, 2018-June 30, 2028.*

Germano, K. M. and Bishop, P. J. (2009). Suitability of amphibians and reptiles for translocation. *Conservation Biology*, 23(1), 7-15.

Gibbons, J. W., Scott, D. E., Ryan, T. J., Buhlmann, K. A., Tuberville, T. D., Metts, B. S., Greene, J. L., Mills, T., Leiden, Y., Poppy, S., and Winne, C. T. (2000). The global decline of reptiles, déjà vu amphibians: reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. *BioScience*, 50(8):653-666.

Guillera-Arroita, G., Ridout, M. S., and Morgan, B. J. T. (2010). Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*, 1:131-139.

Guyer, C. and Bailey, M. A. (1993). Amphibians and reptiles of longleaf pine communities. In *Proceedings of the Tall Timbers Fire Ecology Conference*, 18:139-158.

Guzy, J. C., Halloran, K. M., Homyack, J. A., Thornton-Frost, J. E., and Willson, J. D. (2019). Differential responses of amphibian and reptile assemblages to size of riparian buffers within managed forests. *Ecological Applications,* 29(8).

Hendry, H. and Mann, C. (2017). Camelot–intuitive software for camera trap data management. *BioRxiv*, 203216.

Hilderbrand, R. H., Watts, A. C., and Randle, A. M. (2005). The myths of restoration ecology. *Ecology and Society,* 10(19).

Homyack, J. A., O'Bryan, C. J., Thornton, J. E., and Baldwin, R. F. (2016). Community occupancy of herpetofauna in roadside ditches in a managed pine landscape. *Forest Ecology and Management*, 361:346-357.

Hoss, S. K., Guyer, C., Smith, L. L. and Schuett, G. W. (2010). Multiscale influences of landscape composition and configuration on the spatial ecology of eastern diamond-backed rattlesnakes (*Crotalus adamanteus*). *Journal of Herpetology,* 44:110–123.

Howze, J. M. and Smith, L. L. (2022). Habitat use for two heliothermic lizards in Longleaf pine savannas. *Southeastern Naturalist*, 21(4):246-257.

Howze, J. M. and Smith, L. L. (2021). The influence of prescribed fire on site selection in snakes in the longleaf pine ecosystem. *Forest Ecology and Management,* 481:118703.

Howze, J. M. and Smith, L. L. (2015). Spatial ecology and habitat use of the coachwhip in a Longleaf pine forest. *Southeastern Naturalist*, 14(2):342-350.

Lee, J. H. and Park, D. (2011). Spatial ecology of translocated and resident Amur ratsnakes (*Elaphe schrenckii*) in two mountain valleys of South Korea. *Asian Herpetological Research*, 2(4):223-229.

Lehtinen, R. M. and Galatowitsch, S. M. (2001). Colonization of restored wetlands by amphibians in Minnesota. *American Midland Naturalist,* 145:388–396.

Leiden, Y.A., Dorcas, M.E., and Gibbons, J.W. (1999). Herpetofaunal diversity in coastal plain communities of South Carolina. *J. Elisha Mitchell Society,* 115(4):270-280.

Lindenmayer, D. (2020). Improving restoration programs through greater connection with ecological theory and better monitoring. *Frontiers in Ecology and Evolution*, 8(50).

Lunn, D. J., Thomas, A., Best, N., and Spiegelhalter, D. (2000). WinBUGS– a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing,* 10:325-337.

Martin, S. A., Rautsaw, R. M., Robb, F., Bolt, M. R., Parkinson, C. L., and Seigel, R. A. (2017). Set AHDriFT: applying game cameras to drift fences for surveying herpetofauna and small mammals. *Wildlife Society Bulletin,* 41(4):804-809.

Matthias, L., Allison, M. J., Maslovat, C. Y., Hobbs, J., and Helbing, C. C. (2021). Improving ecological surveys for the detection of cryptic, fossorial snakes using eDNA on and under artificial cover objects. *Ecological Indicators*, 131:108187.

McAlpine, C., Catterall, C. P., MacNally, R., Lindenmayer, D., Reid, J. L., Holl, K. D., Bennett, A. F., Runting, R. K., Wilson, K., Hobbs, R. J., Seabrook, L., Cunningham, S., Moilanen, A., Maron, M., Shoo, L., Lunt, I., Vesk, P., Rumpff, L., Marint, T. G., Thomson, J., and Possingham, H. (2016). Integrating plant and animal-based perspectives for more effective restoration of biodiversity. *Frontiers in Ecology and the Environment,* 14:37-45.

McCleery, R. A., Zweig, C. L., Desa, M. A., Hunt, R., Kitchens, W. M., and Percival, H. F. (2014). A novel method for camera-trapping small mammals. *Wildlife Society Bulletin,* 38(4):887-891.

McIntyre, R. K., McCall, B. B., and Wear, D. N. (2017). The social and economic drivers of the southeastern forest landscape. In *Ecological restoration and management of longleaf pine forests* (pp. 39-68). CRC Press.

Meli, P., Holl, K. D., Rey Benayas, J. M., Jones, H. P., Jones, P. C., Montoya, D., and Moreno Mateos, D. (2017). A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. *Plos one*, 12(2):e0171368.

Munro, N. T., Lindenmayer, D. B., and Fischer, J. (2007). Faunal response to revegetation in agricultural areas of Australia: a review. *Ecological Management and Restoration,* 8:199–207.

Nichols, O. G. and Grant, C. D. (2007). Vertebrate fauna recolonization of restored bauxite mines-Key findings from almost 30 years of monitoring and research. *Restoration Ecology,* 15:S116–S126.

Pacifici, K., Zipkin, E. F., Collazo, J. A., Irizarry, J. I., and DeWan, A. (2014). Guidelines for a priori grouping of species in hierarchical community models. *Ecology and Evolution*, 4(7):877-888.

Palmer, M. A., Ambrose, R. F., and Poff, N. L. (1997). Ecological theory and community restoration ecology. *Restoration Ecology*, 5:291-300.

Perry, R. W., Rudolph, D. C., and Thill, R. E. (2009). Reptile and amphibian responses to restoration of fire-maintained pine woodlands. *Restoration Ecology*, 17(6):917-927.

Plummer, M. (2003). A program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd international workshop on distributed statistical computing.* Vienna, Austria.

R Core Team. (2018). R: A language and environment for statistical computing. R Project for Statistical Computing, Vienna, Austria. www.R-project.org

Ryberg, W. A., Walkup, D. K., Hibbits, T. J., Pittman, W., Porter, V. H., Bowers, B. C., Fielder, C. M., Brown, P., Lopez, R. R., Preston, J. R., Johnson, J. T., and Hagedorn, B. W. (2021). Effective camera trap snake surveys at a rarely accessible longleaf pine savanna. *Herpetological Review,* 52(4):719-724.

Sauer, J. R. and Link W. A. (2002). Hierarchical modeling of population stability and species group attributes from survey data. *Ecology,* 86:1743-1751.

Singh, S., Smyth, A. K., and Blomberg, S. P. (2002). Effect of a control burn on lizards and their structural environment in a eucalypt open-forest. *Wildlife Research*, 29(5):447-454.

Society for Ecological Restoration (International Science and Policy Working Group). (2004). The SER International Primer on Ecological Restoration. Washington, DC: Society for Ecological Restoration.

Steen, D. A., Smith, L. L., Conner, L. M., Litt, A. R., Provencher, L., Hiers, J. K., Pokswinski, S., and Guyer, C. (2013). Reptile assemblage response to restoration of fire-suppressed longleaf pine sandhills. *Ecological Applications,* 23:148–158.

Su, Y.-S. and Yajima, M. (2015). R2jags: A package for running jags from R. R package version 0.03-08. http://CRAN.R-project.org/package=R2jags

Sullivan, B. K., Nowak, E. M., and Kwiatkowski, M. A. (2015). Problems with mitigation translocation of herpetofauna. *Conservation Biology*, 29(1):12-18.

Todd, B. D., Winne, C. T., Willson, J. D., and Gibbons, J. W. (2007). Getting the drift: Examining the effects of timing, trap type, and taxon on herpetofaunal drift fence surveys. *The American Midland Naturalist,* 158(2):292-305.

Todd, B. D., and Andrews, K. M. (2008). Response of a reptile guild to forest harvesting. *Conservation Biology*, 22(3):753-761.

Todd, B. D., Willson, J. D., and Gibbons, J. W. (2010). 'Ecotoxicology of Amphibians and Reptiles.' (CRC Press: Boca Raton, FL.)

Tomlinson, S., Arnall, S. G., Munn, A., Bradshaw, S. D., Maloney, S. K., Dixon, K. W., and Didham, R. K. (2014). Applications and implications of ecological energetics. *Trends in Ecology and Evolution*, 29(5):280-290.

Tuberville, T. D., Norton, T. M., Todd, B. D., and Spratt, J. S. (2008). Long-term apparent survival of translocated gopher tortoises: a comparison of newly released and previously established animals. *Biological Conservation*, 141(11):2690-2697.

United States Department of Agriculture, Natural Resources Conservation Service. (2023). *Longleaf Pine Initiative.* Available online at https://www.nrcs.usda.gov/programs-initiatives/longleaf-pine-initiative. Accessed May 15, 2023.

Uhe, L., Albrecht, K., Schleicher, A., and Engler, J. O. (2020). Adjusting trail cameras to improve monitoring of small open cup nesting birds. *Journal of Ornithology,* 161(3):893-899.

Waldron, J. L., Welch, S. M., Bennett, S. H., Kalinowsky, W. G. and Mousseau, T. A. (2013). Life history constraints contribute to the vulnerability of a declining North American rattlesnake. *Biological Conservation,* 159:530–538.

Ware, S., Frost, C., and Doerr, P. D. (1993). Southern mixed hardwood forest: the former longleaf pine forest. *Biodiversity of the southeastern United States: Lowland terrestrial communities*, 447-493.

Welbourne, D. A. (2013). A method for surveying diurnal terrestrial reptiles with passive infrared automatically triggered cameras. *Herpetological Review,* 44:247–250.

Welbourne, D. J., MacGregor, C., Paull, D., and Lindenmayer, D. B. (2015). The effectiveness and cost of camera traps for surveying small reptiles and critical weight range mammals: a comparison with labour-intensive complementary methods. *Wildlife Research,* 42(5):414-425.

Wortley, L., Hero, J. M., and Howes, M. (2013). Evaluating ecological restoration success: a review of the literature. *Restoration Ecology*, 21(5):537-543.

Zipkin, E. F., DeWan, A., and Andrew Royle, J. (2009). Impacts of forest fragmentation on species richness: a hierarchical approach to community modeling. *Journal of Applied Ecology,* 46(4):815-822.

# Tables

Table 3.1. Characterization of each site surveyed within Alapaha River Wildlife Management Area, Georgia, USA.

| Site | Pine Basal Area (sq ft per acre) | Restoration State | Year Last Burned | Year Thinned | Distance to Remnant (m) |
|---|---|---|---|---|---|
| 1 | 52.15 | Restored | 2022 | 2018 | 1180 |
| 2 | 167.82 | Unrestored | 2022 | NA | 1200 |
| 3 | 55.83 | Restored | 2021 | 2018 | 2390 |
| 4 | 62.07 | Restored | 2022 | 2019 | 1870 |
| 5 | 81.75 | Unrestored | 2021 | 2019 | 2800 |
| 6 | 37.01 | Restored | 2022 | 2020 | 1775 |
| 7 | 67.47 | Restored | 2022 | 2018 | 175 |
| 8 | 55.03 | Restored | 2022 | 2018 | 450 |
| 9 | 46.09 | Restored | 2020 | 2021 | 250 |
| 10 | 7.78 | Remnant | 2022 | NA | 0 |
| 11 | 5.57 | Remnant | 2022 | NA | 0 |
| 12 | 31.59 | Restored | 2021 | 2021 | 865 |
| 13 | 136.85 | Unrestored | 2019 | 2021 | 1920 |
| 14 | 23.28 | Restored | 2022 | NA | 2245 |
| 15 | 42.72 | Restored | 2022 | 2018 | 1200 |
| 16 | 46.28 | Restored | 2021 | 2019 | 2935 |
| 17 | 48.86 | Restored | 2022 | 2020 | 1335 |
| 18 | 116.03 | Unrestored | 2022 | NA | 3310 |
| 19 | 112.77 | Unrestored | 2022 | NA | 1250 |
| 20 | 70.00 | Restored | 2019 | 2020 | 2350 |

Table 3.2. Summary of squamate species captured within Alapaha River Wildlife Management Area, Georgia, USA.

| Scientific name | Figure code name | # Sites | Independent Observations |
|---|---|---:|---:|
| *Anolis carolinensis* | anocar | 18 | 75 |
| *Aspidoscelis sexlineata* | aspsex | 18 | 178 |
| *Coluber constrictor* | colcon | 19 | 189 |
| *Crotalus adamanteus* | croada | 2 | 4 |
| *Heterodon platirhinos* | hetpla | 9 | 19 |
| *Masticophis flagellum* | masfla | 10 | 38 |
| *Nerodia erythrogaster* | nerery | 1 | 1 |
| *Pantherophis alleghaniensis* | panall | 6 | 7 |
| *Pantherophis guttatus* | pangut | 2 | 2 |
| *Pituophis melanoleucus* | pitmel | 1 | 1 |
| *Plestiodon egregius* | pleegr | 3 | 4 |
| *Plestiodon laticeps* | plelat | 4 | 13 |
| *Plestiodon* spp. | plespp | 6 | 36 |
| *Sceloporus undulatus* | sceund | 18 | 224 |
| *Scincella lateralis* | scilat | 13 | 25 |

Table 3.3. Summary of group-level hyper-parameters for occupancy covariates across 15 squamate species detected within Alapaha River WMA, Georgia, USA. Estimates in bold indicate estimates for which the Bayesian p-value (the proportion of simulations in which the estimated occupancy probability had the same sign as the mean) > 0.80.

| Group-level hyper-parameter | | Group | Mean | 95% CI | | Bayesian p-value |
|---|---|---|---|---|---|---|
| Variable | Definition | | | | | |
| $\mu_{BA1}$ | Basal Area | Lizard | 0.541 | -0.963 | 2.600 | 0.736 |
| $\mu_{BA2}$ | Basal Area | Snake | -0.370 | -1.854 | 1.146 | 0.718 |
| $\mu_{B1}$ | Burn | Lizard | 0.312 | -1.274 | 2.694 | 0.605 |
| $\mu_{B2}$ | Burn | Snake | -0.135 | -1.513 | 1.252 | 0.576 |
| $\mu_{D1}$ | Distance | Lizard | -0.288 | -1.897 | 1.233 | 0.668 |
| **$\mu_{D2}$** | **Distance** | **Snake** | **-0.785** | **-2.524** | **0.855** | **0.850** |
| $\mu_{R1}$ | Thin | Lizard | 0.315 | -1.067 | 1.972 | 0.680 |
| **$\mu_{R2}$** | **Thin** | **Snake** | **1.147** | **-0.620** | **3.262** | **0.886** |

Table 3.4. Summary of species-specific estimates for occupancy covariates for 15 squamate species detected within Alapaha River WMA. Estimates include 95% credible intervals and Bayesian p-values (the proportion of simulations in which the estimated occupancy probability had the same sign as the mean). Estimates in bold indicate estimates for which the Bayesian p-value > 0.80.

| Species | Species-specific parameter | Mean | 95% CI | | Bayesian p-value |
|---|---|---|---|---|---|
| *Anolis carolinensis* | Basal Area | 0.545 | -1.646 | 3.396 | 0.657 |
| | Burn | 0.479 | -1.739 | 3.207 | 0.630 |
| | Distance | -0.294 | -2.610 | 2.173 | 0.622 |
| | Thin | 0.540 | -1.466 | 2.721 | 0.691 |
| *Aspidoscelis sexlineata* | Basal Area | 0.094 | -2.195 | 2.893 | 0.506 |
| | Burn | 0.619 | -1.518 | 3.227 | 0.684 |
| | Distance | -0.911 | -3.717 | 1.662 | 0.761 |
| | Thin | 0.154 | -1.921 | 2.499 | 0.541 |
| *Coluber constrictor* | Basal Area | 0.018 | -1.708 | 2.313 | 0.465 |
| | Burn | 0.377 | -1.354 | 2.299 | 0.651 |
| | Distance | -0.258 | -2.119 | 1.962 | 0.632 |
| | **Thin** | **1.195** | **-0.918** | **3.661** | **0.854** |
| *Crotalus adamanteus* | Basal Area | -0.552 | -3.601 | 2.135 | 0.702 |
| | Burn | -0.483 | -2.615 | 1.731 | 0.674 |
| | Distance | -0.605 | -4.204 | 3.030 | 0.685 |
| | Thin | 0.679 | -1.955 | 3.817 | 0.635 |
| *Heterodon platirhinos* | **Basal Area** | **-0.789** | **-2.406** | **0.612** | **0.868** |
| | Burn | -0.103 | -1.875 | 1.565 | 0.538 |
| | **Distance** | **-0.844** | **-2.629** | **0.683** | **0.864** |
| | **Thin** | **1.579** | **-0.325** | **3.991** | **0.946** |
| *Masticophis flagellum* | Basal Area | -0.511 | -2.111 | 0.953 | 0.765 |
| | **Burn** | **-0.740** | **-2.550** | **0.771** | **0.810** |
| | **Distance** | **-1.892** | **-4.560** | **-0.160** | **0.984** |
| | **Thin** | **1.645** | **-0.360** | **4.030** | **0.936** |
| *Nerodia erythrogaster* | Basal Area | -0.660 | -3.823 | 1.846 | 0.723 |
| | Burn | 0.020 | -2.366 | 2.368 | 0.506 |
| | **Distance** | **-1.235** | **-5.047** | **1.952** | **0.807** |
| | Thin | 1.042 | -1.665 | 4.082 | 0.759 |

| Species | Species-specific parameter | Mean | 95% CI | | Bayesian p-value |
|---|---|---|---|---|---|
| *Pantherophis alleghaniensis* | Basal Area | -0.482 | -3.164 | 2.242 | 0.697 |
| | Burn | 0.158 | -1.695 | 2.234 | 0.557 |
| | Distance | 0.080 | -2.248 | 3.008 | 0.484 |
| | Thin | 1.010 | -1.642 | 3.924 | 0.757 |
| *Pantherophis guttatus* | Basal Area | 0.362 | -2.870 | 2.176 | 0.341 |
| | Burn | -0.092 | -2.417 | 2.216 | 0.538 |
| | **Distance** | **-1.385** | **-5.446** | **1.844** | **0.831** |
| | **Thin** | **1.238** | **-1.431** | **4.129** | **0.810** |
| *Pituophis melanoleucus* | Basal Area | 0.180 | -1.831 | 3.215 | 0.493 |
| | Burn | -0.225 | -2.523 | 2.083 | 0.579 |
| | Distance | -0.952 | -4.739 | 2.575 | 0.759 |
| | **Thin** | **1.371** | **-1.358** | **4.274** | **0.832** |
| *Plestiodon egregius* | Basal Area | -0.255 | -3.976 | 3.125 | 0.567 |
| | Burn | 0.018 | -2.431 | 2.975 | 0.472 |
| | Distance | -0.866 | -3.867 | 1.299 | 0.773 |
| | Thin | 0.848 | -1.399 | 3.107 | 0.775 |
| *Plestiodon laticeps* | Basal Area | 0.687 | -2.715 | 4.933 | 0.653 |
| | Burn | 0.098 | -2.442 | 3.215 | 0.491 |
| | Distance | 0.486 | -2.049 | 3.911 | 0.611 |
| | Thin | 0.085 | -2.201 | 2.668 | 0.507 |
| *Plestiodon* spp | **Basal Area** | **1.368** | **-0.661** | **5.511** | **0.853** |
| | Burn | 0.518 | -1.580 | 3.902 | 0.547 |
| | Distance | 0.181 | -1.493 | 1.774 | 0.602 |
| | Thin | -0.003 | -1.660 | 1.814 | 0.513 |
| *Sceloporus undulatus* | Basal Area | 0.901 | -1.265 | 3.837 | 0.765 |
| | Burn | 0.227 | -1.683 | 2.710 | 0.550 |
| | Distance | -0.946 | -3.591 | 1.550 | 0.790 |
| | Thin | 0.656 | -1.254 | 2.734 | 0.739 |
| *Scincilla lateralis* | **Basal Area** | **1.460** | **-1.236** | **5.569** | **0.817** |
| | Burn | 0.582 | -1.563 | 3.339 | 0.658 |
| | Distance | -0.946 | -2.495 | 2.362 | 0.591 |
| | Thin | 0.360 | -1.715 | 2.597 | 0.627 |

# Figures

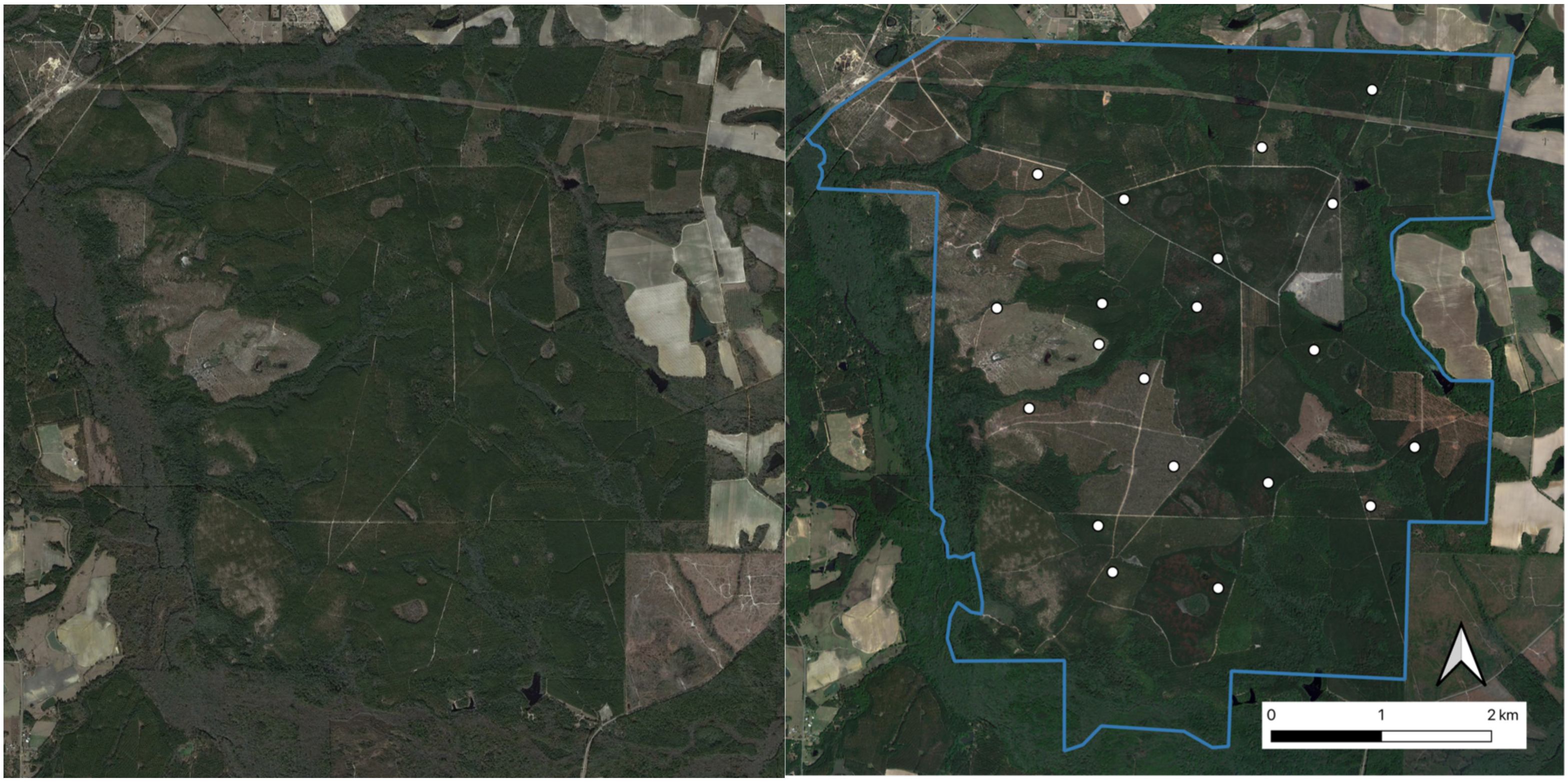

Figure 3.1. Aerial image of Alapaha River Wildlife Management Area, Iwrin County, GA, USA in December 2014 (left) and April 2019 (right) including the locations of the 20 sites surveyed during this study.

Figure 3.2. Modified AHDriFT system at Alapaha River Wildlife Management Area in Irwin County, Georgia, USA. The wildlife camera housing sits in the center of the Y-shaped drift fence array.

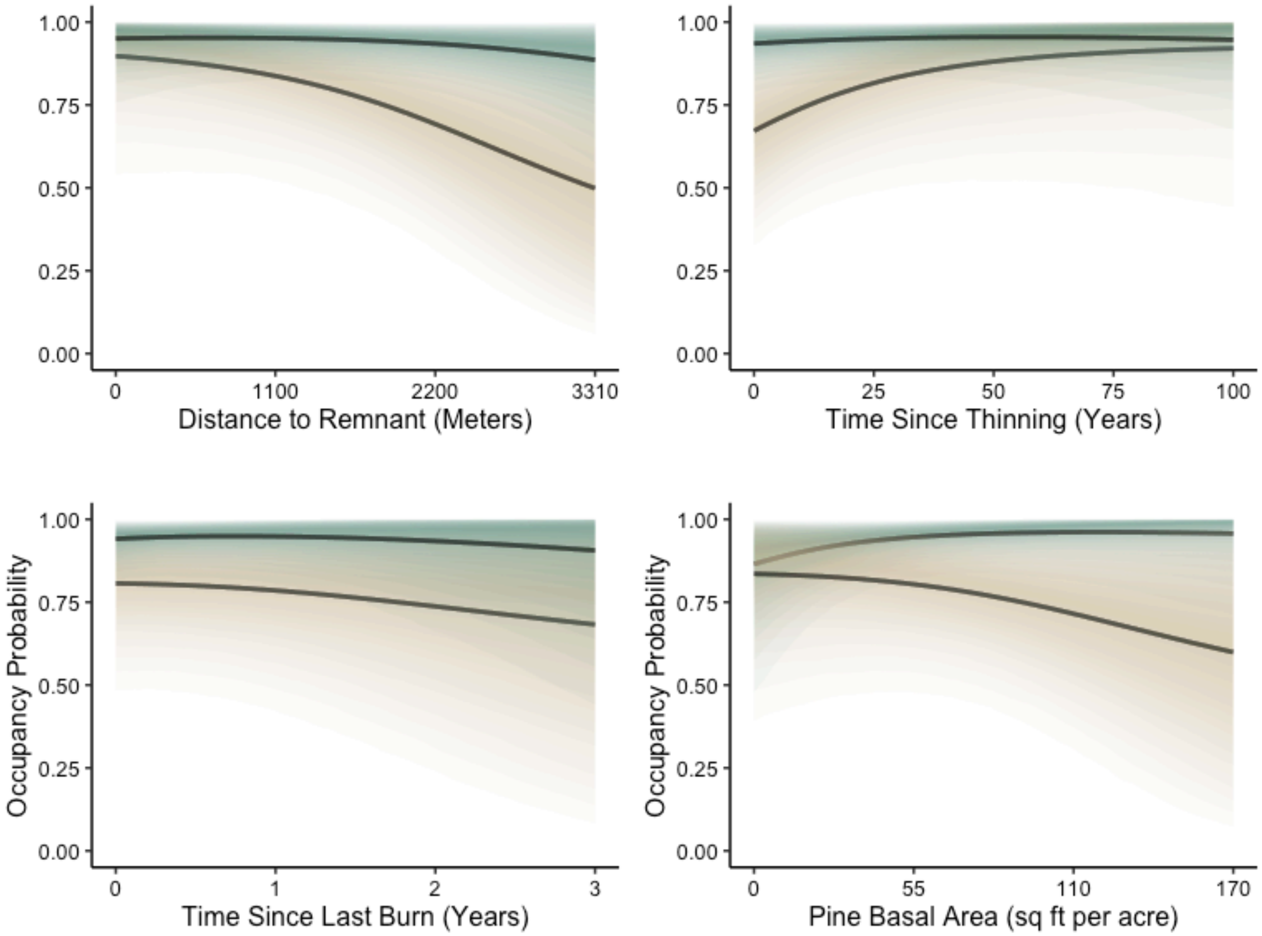

Figure 3.3. Mean estimates of the occupancy probability across snakes (brown) and lizards (green) versus four habitat covariates recorded at Alapaha River WMA in Irwin County, Georgia, USA. Shading denotes 95% Bayesian credible intervals at five percent increments.

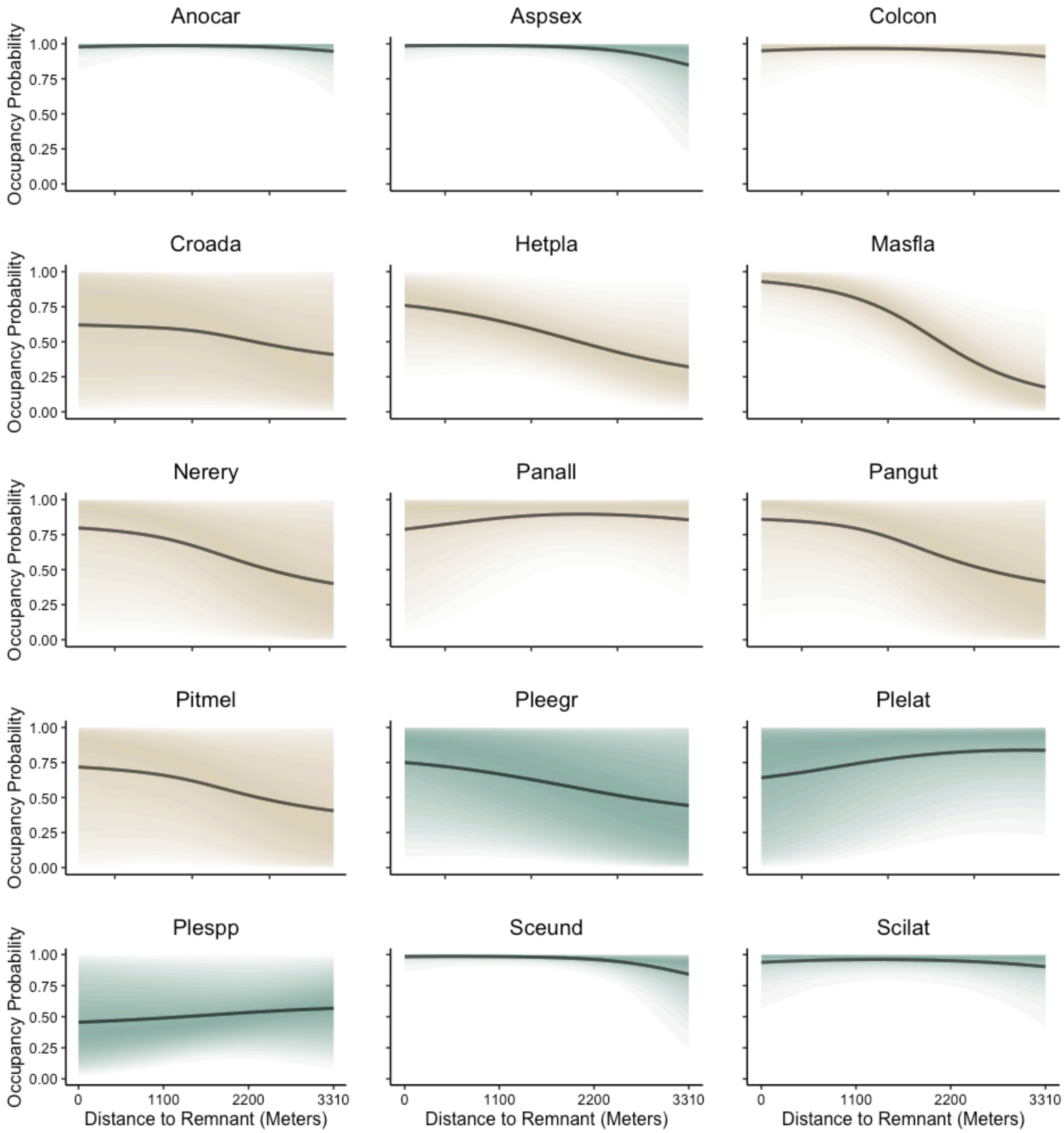

Figure 3.4. Mean species-specific estimates of the occupancy probability for 15 squamate species detected in ARWMA versus distance to remnant "natural" habitat in meters. Shading denotes 95% Bayesian credible intervals at five percent increments.

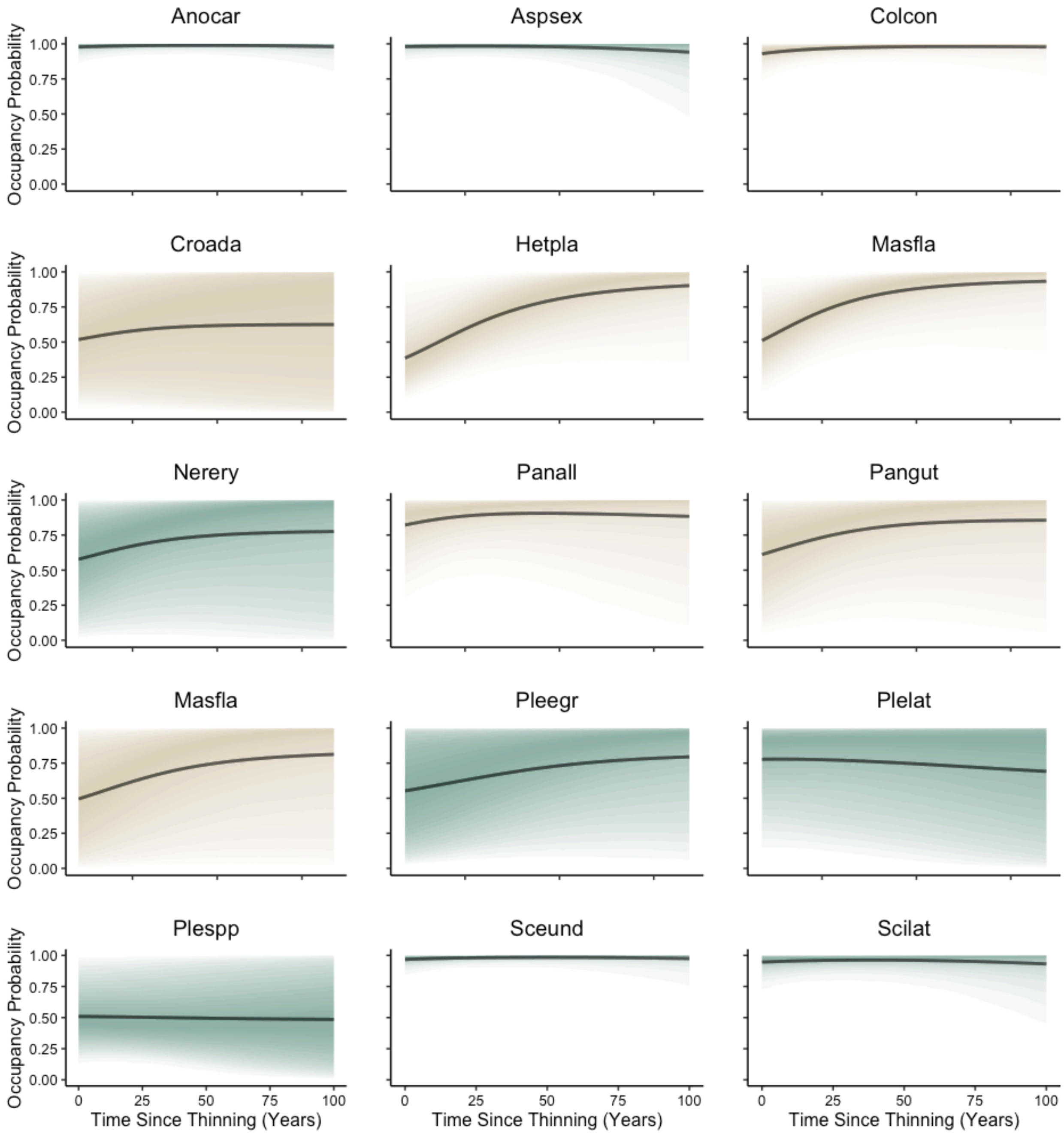

Figure 3.5. Mean species-specific estimates of the occupancy probability for 15 squamate species detected in ARWMA versus time since the stand was thinned in years. Shading denotes 95% Bayesian credible intervals at five percent increments.

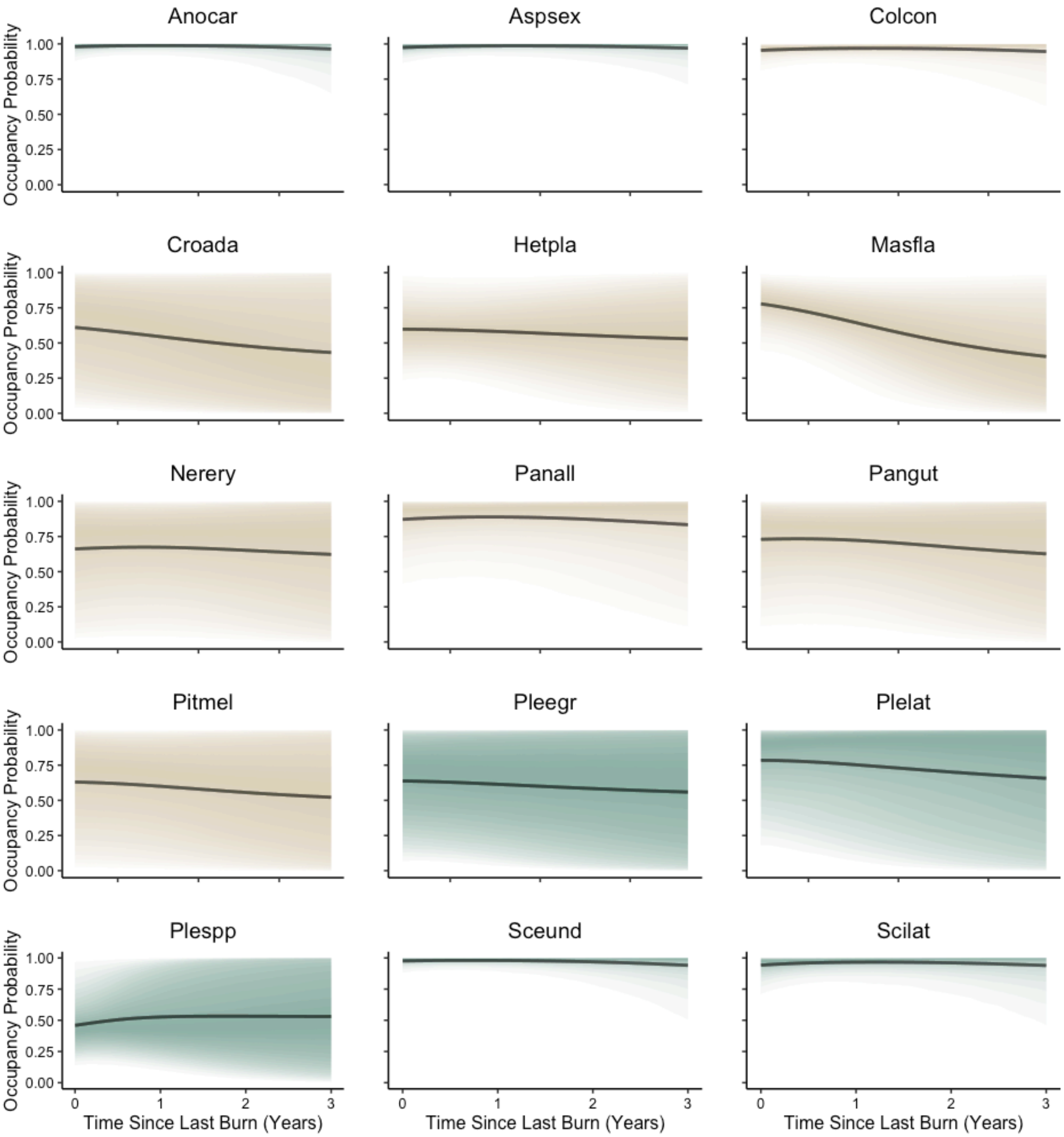

Figure 3.6. Mean species-specific estimates of the occupancy probability for 15 squamate species detected in ARWMA versus the time since the last prescribed fire in years. Shading denotes 95% Bayesian credible intervals at five percent increments.

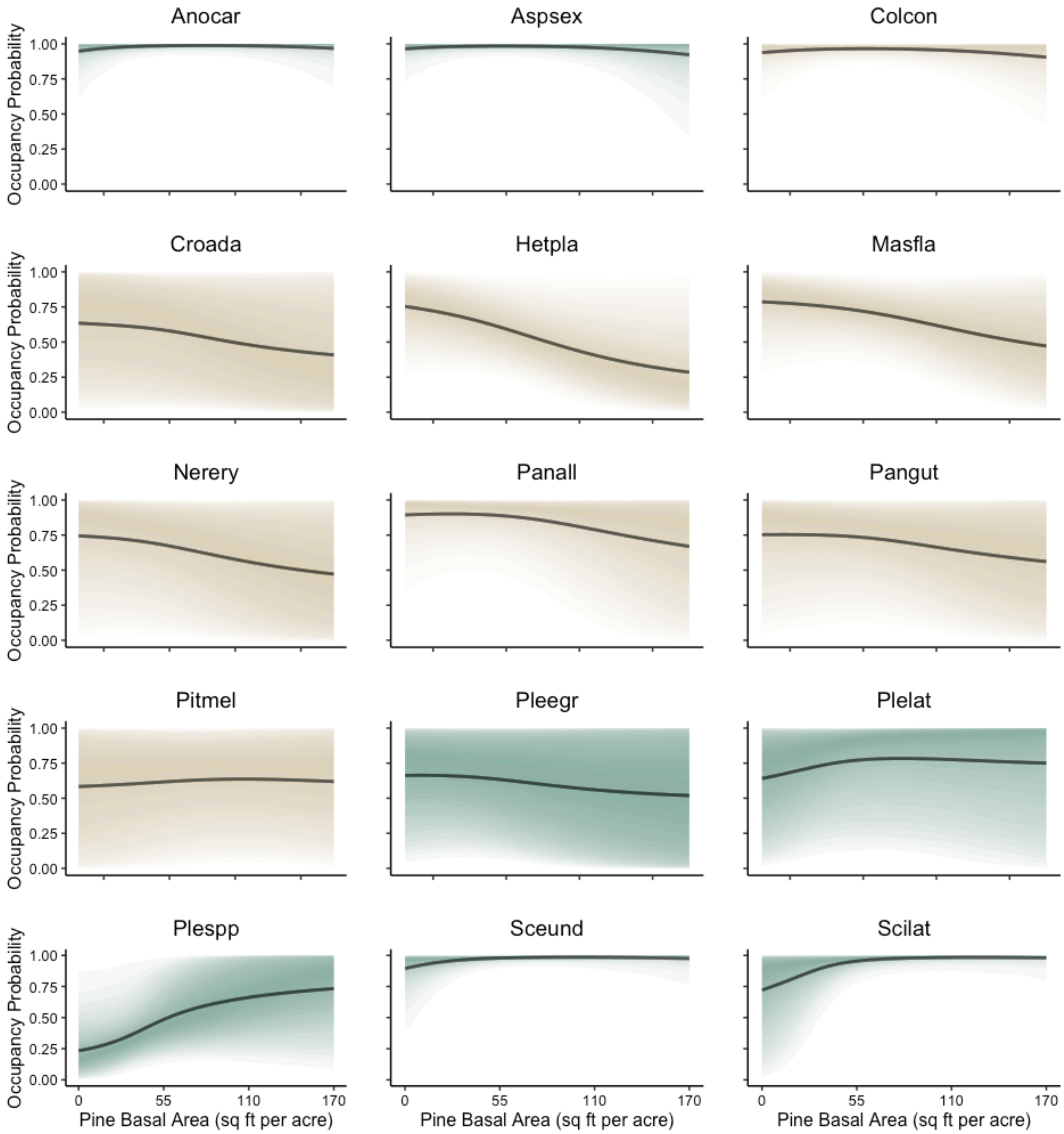

Figure 3.7. Mean species-specific estimates of the occupancy probability for 15 squamate species detected in ARWMA versus pine basal area of a stand in square feet per acre. Shading denotes 95% Bayesian credible intervals at five percent increments.

# CHAPTER 4

# CONCLUSIONS

## *Use of wildlife cameras for studying herpetofauna*

Our lab and field tests of wildlife cameras demonstrated the utility of remote monitoring systems for studying some species of herpetofauna. This was the first study to directly assess the detection of representative species of herpetofauna by wildlife cameras. The top-performing passive infrared (PIR) camera models detected medium-bodied snake species ~50% of the time even when the snakes were at the same temperature as the substrate and neared 100% detection rates as the temperature difference between the snake and the substrate increased. While wildlife cameras were less effective at detecting small snakes and frogs, these animals still triggered the cameras up to 50% of the time they passed through the system if they could achieve a temperature differential. These patterns of laboratory detection were consistent with patterns of detection of amphibians and reptiles when deployed in the field. Most field detections were of medium and larger-bodied snakes and diurnal reptiles such as skinks, anoles, fence lizards, and racerunners.

When deployed, PIR wildlife cameras generated five times more observations and documented more species of herpetofauna than traditional visual encounter surveys with cover boards. Additionally, PIR cameras were seven times more efficient, producing 6.12 herpetofauna observations per person-hour of work compared to the 0.88 herpetofauna observations per person-hour generated using the traditional method. The AHDriFT camera system tested in this study can drastically reduce the effort required to monitor snakes and other large or diurnal herpetofauna compared to the effort required to install and monitor pitfall or funnel traps or conduct visual encounter surveys using roadways or cover boards. No wildlife was harmed using this method, compared to the significant effort required to prevent harm to or death of target and non-target species when using pitfall or funnel traps (Enge 2001). Camera traps can be used for more than just studies of abundance and richness. Mark-recapture studies traditionally rely on trapping to identify individuals of herpetofauna species; however, recent studies have successfully identified and tracked individuals using camera traps (Moore *et al.* 2020). While more research is needed to make this method widely applicable, especially for small, nocturnal species, there is strong potential for camera traps to expand herpetological research worldwide.

When considering that the time required for maintenance and data collection averaged only 2 minutes per site per visit, the AHDriFT system provides a feasible way to implement a long-term herpetofauna monitoring program at multiple locations. This observation is not meant to discourage the continued use of traditional monitoring practices, but to provide researchers and land managers with options and identify wildlife cameras as a resource for long-term monitoring of multiple sites simultaneously for species with low detectability. In addition to herpetofauna, the modified AHDriFT camera systems detected other small wildlife species at ARWMA including small mammals, birds, and invertebrates (Appendix 2.1). Our findings indicate that passive monitoring using wildlife cameras has strong potential to reduce barriers to implementing long-term monitoring projects aiming to study herpetofauna and other small wildlife species.

The inclusion of time-lapse photography significantly increased the average laboratory detection rate of small snake species and would likely also have increased the detection rate of frogs. Therefore, using a combination of PIR and timelapse triggers could be effective for surveying for a wider range of herpetofauna including smaller and nocturnal species provided researchers have the resources to collect and process the high volume of images produced using timelapse. Our results are encouraging for the monitoring of moderate and larger-bodied and diurnal reptiles and should incentivize the development of AI for high-throughput processing of images from wildlife cameras to maximize the effectiveness of wildlife cameras for studying herpetofauna.

Importantly, our results demonstrated that different camera models can vary in their ability to detect herpetofauna, with detection rates spanning 20% to 60%. In our highly controlled environment with uniform backgrounds and guides directing animals underneath the sensor and lens of the cameras, differences in detection rate between models were substantial. Therefore, when utilizing PIR wildlife cameras to study herpetofauna or other similar wildlife, it is necessary to measure the detection rates of target species by a particular camera model. The prices of wildlife cameras vary significantly, with the average camera costing $100 to $200 (Trolliet *et al.* 2014). Therefore, when detection rates are comparable, each camera model's cost might be considered a criterion to reduce costs or maximize coverage. Our results did not suggest detection was correlated with cost, but we encourage those who plan to use wildlife cameras to monitor herpetofauna to consider detection rates and cost when selecting a camera model.

### *Short-Term Responses of Squamates to Forest Restoration at the Alapaha River Wildlife Management Area*

Our estimates of squamate occupancy at ARWMA suggested that some snake species may be responding positively to management actions, though uncertainty was high and variable among species. Lizard species showed limited evidence of any relationship to management. No species showed signs of significant, negative responses to management. Snake occupancy at sites within ARWMA was positively correlated with proximity to remnant patches of habitat. The increased occupancy of snakes in areas closer to the remnant habitat potentially indicates the gradual dispersal of organisms from within the remnant habitat to surrounding areas that have since been restored. This result demonstrates the potential importance of creating connected systems of habitat over isolated patches to increase the chance of reptile colonization and persistence in restored habitats. This may also indicate that restoration of unoccupied habitats that are too far from remnant occupied sites to be colonized naturally will require reintroductions of some species as a component of restoration efforts. Mean estimated occupancy probability was higher in later posttreatment stands for several snake species, consistent with other studies that show reptile communities within restored patches are indistinguishable from remnant patches late posttreatment (Steen *et al.* 2013). Our estimates and those of other studies demonstrate it may take years or decades before restoration actions increase the occupancy of some species in an area. When combined with the effect of isolation on the occupancy of restored areas, a restored site that is isolated from remnant habitat could have a protracted period between restoration and recovery of fauna, particularly for dispersal limited species. This information is important to land managers because the time required to see increases in occupancy could exceed the extent of the monitoring project, which could lead to the devaluation of effective restoration measures.

We saw little evidence management actions were having negative effects on the occupancy of many species. Cases of recent or high frequency burning, basal area reduction, or time since thinning being associated with reduced occupancy were generally limited to 1-3 species and usually had low statistical support. As discussed above, this could be an indication that the time since restoration is not yet long enough to positively influence the occupancy of some species. Additionally, this result could support the implementation of groundcover restoration, disease treatment, and/or targeted invasive species removal to create more suitable habitats for some fauna. Therefore, we believe that – in the near term – the evidence suggests that management actions to restore pine savanna conditions on ARWMA range from positive to benign for squamate species and warrant continuation.

Herpetofauna are a notoriously difficult group of taxa to study, and the combination of passive monitoring and estimation using a hierarchical Bayesian community occupancy model has the potential to improve our ability to manage these species. This method allows estimates to be made about species that are detected infrequently and would otherwise be inestimable (Sauer and Link 2002). Despite cameras being deployed for a full 11 months, occupancy and detection probability were extremely low for some species, which would have influenced the precision and accuracy of a single-species occupancy model (Guillera-Arroita et al. 2010). Land managers should therefore consider that hierarchical multi-species occupancy or abundance models can lead to more precise and efficient monitoring of the recovery of threatened and data-limited species such as herpetofauna.

This study has several limitations. The low numbers of amphibians detected on cameras may reflect a low abundance of amphibians in the terrestrial areas we monitored; however, we also failed to detect any small snake species during this study despite their known presence at ARWMA (Brown and Maerz, personal obs.). Our laboratory study suggests that at least some part of the low detection of amphibians and small snake species in the field was due to the relatively low detection rate of these species by PIR cameras. Targeting these types of species may require the use of time-lapse, though image processing may limit this potential. Alternatively, AIR triggers might be needed to sufficiently detect small, nocturnal species. Due to the observational nature of this study, there may be environmental factors influencing the study species that we were unable to account for. The non-manipulative nature of the study design also meant there were very few patches within ARWMA that met the criteria of "unrestored" according to GADNR's restoration goals. As restoration of longleaf pine savanna is an ongoing practice, it is both feasible and necessary to conduct future experimental studies that control which restoration actions are implemented and where while closely monitoring the response of herpetofauna. Finally, the loss of several cameras due to prescribed fire and flooding may have caused us to miss detecting some of the rarer species observed during the study period and therefore affected our model estimates.

To increase the feasibility of utilizing the AHDriFT method on publicly managed landscapes, we strongly encourage the development of fire-proof camera housing. We also recommend using hardware cloth or metal sheathing in place of silt fencing for the drift fences to make the systems more resilient to fire and other management actions. Directly measuring the responses of fauna to restoration actions is the most assured way to determine whether management actions are recreating functional, self-sustaining ecosystems. While our study demonstrated that restoration actions are not harming herpetofauna on ARWMA in the short term, longer-term monitoring is necessary to determine whether populations will recolonize and persist at this site within the restored pine savannas. Building on this work, future studies should aim to expand the study of restoration impacts on herpetofauna to a larger, metacommunity scale, and monitoring efforts should be expanded beyond ARWMA to other restored and remnant pine savannas. The AHDriFT method would be extremely suitable for an ambitious study of this nature and has strong potential to reduce barriers to implementing long-term monitoring projects aiming to study herpetofauna and other small wildlife species.

# Literature Cited

Enge, K. M. (2001). The pitfalls of pitfall traps. *Journal of Herpetology,* 35:467-478.

Guillera-Arroita, G., Ridout, M. S., and Morgan, B. J. T. (2010). Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*, 1:131-139.

Moore, H. A., Champney, J. L., Dunlop, J. A., Valentine, L. E., and Nimmo, D. G. (2020). Spot on: Using camera traps to individually monitor one of the world's largest lizards. *Wildlife Research*, 47(4):326-337.

Sauer, J. R. and Link W. A. (2002). Hierarchical modeling of population stability and species group attributes from survey data. *Ecology* 86:1743-1751.

Steen, D. A., Smith, L. L., Conner, L. M., Litt, A. R., Provencher, L., Hiers, J. K., Pokswinski, S., and Guyer, C. (2013). Reptile assemblage response to restoration of fire-suppressed longleaf pine sandhills. *Ecological Applications,* 23:148–158.

Trolliet F, Vermeulen C, Huynen MC, Hambuckers A (2014) Use of camera traps for wildlife studies: a review. *Biotechnologie, Agronomie, Société et Environnement* 18(3).

Appendix 2.1. Total numbers of each taxon detected at 20 patches within Alapaha River Wildlife Management Area from April 2022 to April 2023. These values represent the number of unique trigger events, not the total number or the number of unique animals detected.

| | | **Scientific name** | **# Sites** | **# Observations** |
|---|---|---|---|---|
| **Reptilia** | | | | |
| | Squamata | | 4 | 6 |
| | | *Anolis carolinensis* | 18 | 75 |
| | | *Aspidoscelis sexlineata* | 18 | 178 |
| | | *Coluber constrictor* | 19 | 189 |
| | | *Crotalus adamanteus* | 2 | 4 |
| | | *Heterodon platirhinos* | 9 | 19 |
| | | *Masticophis flagellum* | 10 | 38 |
| | | *Nerodia erythrogaster* | 1 | 1 |
| | | *Pantherophis alleghaniensis* | 6 | 7 |
| | | *Pantherophis guttatus* | 2 | 2 |
| | | *Pituophis melanoleucus* | 1 | 1 |
| | | *Plestiodon egregius* | 3 | 4 |
| | | *Plestiodon laticeps* | 4 | 13 |
| | | *Plestiodon* spp. | 6 | 36 |
| | | *Sceloporus undulatus* | 18 | 224 |
| | | *Scincilla lateralis* | 13 | 25 |
| | Testudines | | | |
| | | *Gopherus polyphemus* | 2 | 2 |
| | | *Terrapene carolina* | 1 | 1 |
| Amphibia | | | | |
| | Anura | | | |
| | | *Anaxyrus quercicus* | 1 | 1 |
| | | *Anaxyrus terrestris* | 2 | 2 |
| | | *Lithobates catesbeiana* | 1 | 1 |
| | | *Lithobates sphenocephalus* | 1 | 1 |

|  |  |  |  |  |
|---|---|---|---|---|
|  |  | *Pseudacrus crucifer* | 1 | 1 |
|  |  | *Scaphiopus holbrookii* | 2 | 7 |
|  | Caudata |  |  |  |
|  |  | *Ambystoma tigrinum* | 1 | 1 |
| Aves |  |  |  |  |
|  |  | *Regulus calendula* | 3 | 6 |
|  |  | *Thryothorus ludovicianus* | 12 | 160 |
| Mammalia |  |  |  |  |
|  | Rodentia |  | 16 | 298 |
|  |  | *Peromyscus gossypinus* | 13 | 73 |
|  |  | *Reithrodontomys humulis* | 1 | 1 |
|  |  | *Sigmodon hispidus* | 4 | 41 |
|  |  | *Soricidae* spp. | 3 | 34 |
| Arachnida |  |  |  |  |
|  | Araneae |  | 15 | 250 |
|  | Opiliones |  | 4 | 20 |
|  | Scorpiones |  | 3 | 3 |
| Blattodea |  |  | 2 | 2 |
| Chilopoda |  |  | 4 | 7 |
| Insecta |  |  |  |  |
|  | Coleoptera |  | 3 | 3 |
|  | Diptera |  | 5 | 65 |
|  | Heteroptera |  | 1 | 3 |
|  | Hymenoptera |  | 19 | 254 |
|  | Lepidoptera |  | 7 | 28 |
|  | Orthoptera |  | 14 | 86 |