

USING AN AGENT-BASED MODELLING APPROACH TO DESCRIBE JUVENILE  
GOPHER FROG (*RANA CAPITO*) MOVEMENT PATTERNS AND INFORM FUTURE  
REINTRODUCTION STRATEGIES

by

BENJAMIN JOSEPH THESING

(Under the Direction of Nathan P. Nibbelink)

ABSTRACT

The gopher frog (*Rana capito*) is listed as a Species of Greatest Conservation Need in all states in which it occurs and is currently petitioned to be listed under the Endangered Species Act. Efforts to conserve and manage this species have focused on wetland restoration, population monitoring, and captive-rearing for reintroduction. We conducted radiotelemetry on captive-reared juveniles to parameterize an agent-based model that simulates juvenile gopher frog movement. We fit the model to observed data by adjusting a gopher tortoise burrow detection parameter and comparing the distributions of net-displacement distances from modelled individuals and those from tracked individuals. Net-displacement distributions corresponding to a burrow detection radius of 1 meter were not different from observed data ( $p > .05$ ). We used this movement model to predict landscape connectivity of gopher frogs based on burrow location and suitable habitat on Alapaha River Wildlife Management Area to inform future reintroduction strategies.

INDEX WORDS: Gopher frog; dispersal; agent-based model; reintroduction; telemetry; conservation; wildlife

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May 2023

## DEDICATION

I dedicate this thesis to my parents, Michael and Michelle Thesing, and my sister, Annika Thesing. You have been the best family I could hope to have. Thank you for your unwavering support of my goals and future.

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## CHAPTER 1

### INTRODUCTION

Ecosystem degradation and habitat loss are primary pathways by which species experience severe population declines or even extinctions (Jenkins et al. 2013; Reece and Noss 2014; Cox et al. 2022). Where degradation and loss of habitat has occurred, restoration and active management has been successful in rebuilding and maintaining suitable habitat (King et al. 2009). However, the success of these actions is dependent on careful research efforts that are time and resource intensive (Ehrenfeld 2000). This is problematic because species monitoring efforts have revealed that losses can occur at a rate that surpasses the ability of habitat management to buffer declines (Gorman et al. 2013; Stuhldreher and Fartmann 2014). Furthermore, wildlife populations experiencing severe declines are often unable to naturally recover due to isolation and genetic loss (Frankham and Ralls 1998). Researchers frequently use reintroduction programs to coincide with habitat restoration and management to establish a population of a target species at a site of local extirpation or to mitigate rapid individual losses of an existing one (Houde et al. 2015). While there are many successful examples of this practice, reintroduction programs are notoriously time and resource intensive (Snyder et al. 1996; Griffiths and Pavajeau 2008; Houde et al. 2015). Thus, research designed to optimize reintroduction programs based on the natural history, physiology, and ecology of the species in question can increase chances of success.

Statistical models are often used to predict trends in wildlife ecology and consequences of management actions (Sandford et al. 2017; Wightman et al. 2022; Gaya et al. 2023). Models

that predict animal movement have been especially effective at helping researchers study species' behavior and identify conservation and management priorities (Runge et al. 2014; Lannoo et al. 2017; Kohl et al. 2018; Scroggie et al. 2019). Agent-based models (hereafter ABMs) have proven effective for studying animal movement and habitat use because they inherently possess the perspective to model individual variability in behavior (Railsback and Johnson 2011; Albeke et al. 2015; Railsback and Grimm 2019; McIntire and Maerz 2019, Burrow et al. 2023). Empirical models that derive outcomes from population means cannot account for this variability and therefore pave the way for ABMs to describe patterns generated by individual behavior (Railsback and Grimm 2019). While spatially explicit habitat suitability models provide a map of predicted suitable habitat and dynamic population models allow researchers to predict changing vital rates, inferring from separate models is challenging. ABMs take a step towards mitigating these challenges by introducing a spatially explicit framework to quantify adaptive decisions of an individual and observe how patterns emerge throughout the system under a flexible set of variables (Dunning et al. 1995; Albeke et al. 2015). A study on amphibian populations in a dynamic floodplain system demonstrates this utility. The ABM approach facilitated spatially explicit interactive subsystems varying within the model to simulate how changing climate, weather, and hydrodynamics affected site selection and population dynamics of the moor frog (*Rana arvalis*) (Dick and Ayllon 2017). The unique ability of an ABM framework to handle this complexity makes it a highly suitable tool to apply to studying amphibians.

Due to habitat loss, habitat fragmentation, and degradation of suitable breeding wetlands, the Carolina gopher frog (*Rana capito*) has experienced declines throughout its range and is thus the target of a reintroduction program in Georgia, USA (Terrell and Maerz 2016). The Gopher

Frog is a medium sized ranid frog (est. adult size 2.5 – 3.5 in.) that is endemic to the southeastern United States and which primarily occupies pine savannas such as the long leaf pine (*Pinus palustris*), flatwoods, and sandhills habitat in the Atlantic coastal plain (Jensen et al. 2008). The Gopher Frog is listed as a Species of Greatest Conservation Need (SGCN) in all states in which it occurs (Georgia Department of Natural Resources 2015; North Carolina Wildlife Resources Commission 2015; South Carolina Department of Natural Resources 2015; Alabama Department of Conservation and Natural Resources 2015; Florida Fish and Wildlife Conservation Commission 2019) and is currently petitioned for listing under the federal Endangered Species Act (16 U.S.C. §§ 1531-1540 [1988]). Recent restoration and management efforts have focused on restoring breeding wetlands and the surrounding upland habitat while reintroduction of juvenile gopher frogs has attempted to revitalize local populations across the state of Georgia. Studies and field observations of reintroduced and wild-born juvenile gopher frogs suggest that survival of newly metamorphosed individuals is correlated with the availability of underground refugia (Roznik and Johnson 2009). Gopher frogs have been observed using stump holes, small mammal burrows, and gopher tortoise (*Gopherus polyphemus*) burrows before, during, and after dispersal-type movements (Roznik and Johnson 2009; Humphries and Sisson 2012, Hunt 2019). Refugia can provide protection from depredation, a stable microclimate, and food (Jensen et al. 2008). Unlike adult frogs, which have been shown to possess site fidelity to refugia when migrating to and from breeding wetlands, juvenile amphibians are assumed to be naïve with respect to their new landscape and thus show a higher degree of dispersal (Rothermel 2004; Semlitsch 2008; Pittman et al. 2014). Additionally, non-breeding dispersal in many pond-breeding amphibians seems to occur primarily before individuals reach sexual maturity (Semlitsch 2008). However, knowledge of refugia use and non-breeding terrestrial movement

patterns in gopher frogs is incomplete (Roznik and Johnson 2009a; Roznik and Johnson 2009b; Hunt 2019). Thus, understanding patterns of subadult movement and survival may be critical for planning successful reintroduction programs. Additionally, spatially explicit models that incorporate movement and survival under a variety of landscape scenarios can help managers create effective restoration and reintroduction strategies.

Movement models informed by telemetry data suggest that gopher frogs exhibit random dispersal with regards to direction of exit from a wetland and turning angles during movement (Hunt 2019). However, these models lack parameters that directly affect cohort survival (e.g., predation, habitat variables) and thus do not reveal the mechanistic patterns that can cause variability within these factors. This inhibits our ability to accurately simulate terrestrial movement under different management scenarios. Since dispersal is essential to population and metapopulation survival, characterizing patterns associated with dispersal and observing the decision-making of individuals could be critical to informing future reintroduction efforts. Using ABMs to conceptualize and track patterns associated with movement, quantity of available refugia, and spatial arrangement of refugia would likely improve our ability to reintroduce juvenile gopher frogs in locations that maximize long term persistence on the landscape.

### *Thesis Objectives*

The overall goal of this project was to use agent-based modelling to simulate patterns of dispersal and refugia use of reintroduced juvenile gopher frogs to inform future reintroduction and management efforts. The objective of Chapter 2 was to use data from radiotelemetry to parameterize an agent-based model that accurately simulates juvenile gopher frog dispersal from a single release point. In Chapter 2, we build this model and fit the model to observed patterns of

juvenile gopher frog movement. Chapter 3 focuses on applying the movement model to different gopher frog reintroduction scenarios at Alapaha River Wildlife Management Area in Georgia, USA. Specifically, we explore the relative connectivity of target wetlands with respect to the dispersal potential of juvenile gopher frogs under different release scenarios. This approach can be used to inform both reintroduction strategies as well as land management of the property to improve gopher frog metapopulation persistence.

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## CHAPTER 2

### AN AGENT-BASED MODELLING APPROACH TO SIMULATE PATTERNS OF JUVENILE GOPHER FROG (*RANA CAPITO*) DISPERSAL<sup>1</sup>

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## **Abstract**

The gopher frog (*Rana capito*) is listed as a Species of Greatest Conservation Need in all states in which it occurs and is currently petitioned to be listed under the Endangered Species Act. Efforts to conserve and manage this species have focused on wetland restoration, population monitoring, and captive-rearing for reintroduction. We conducted radiotelemetry on captive-reared juveniles to parameterize an agent-based model that simulates juvenile gopher frog movement. We fit the model to observed data by adjusting a gopher tortoise burrow detection parameter and comparing the distributions of net-displacement distances from modelled individuals and those from tracked individuals. Net-displacement distributions corresponding to a burrow detection radius of 1 meter were not different from observed data ( $p > .05$ ).

## **Introduction**

Conservation actions are often shaped by scientific knowledge regarding species' habitat use (Fraser et al. 2018; Hays et al. 2019; Kays et al. 2015; McGowan et al. 2017). For example, species reintroduction plans are commonly used to reinforce a declining population and are often implemented through the translocation of individuals onto a novel, yet presumed suitable, landscape (Seddon et al. 2014). Knowledge of movement and habitat use of these individuals is necessary to ensure their long-term survival and population viability (IUCN 2013). Thus, research based on the natural history, physiology, and ecology of a species can optimize reintroduction and further increase chances of success.

Captive rearing of species followed by reintroduction to native habitat is a tactic that has been developed to mitigate local extirpation and revitalize declining populations while ecosystem restoration and management efforts are in effect (Snyder et al. 1996; Griffiths and Pavajeau 2008; Houde et al. 2015). These methods have proved successful with many species, but the process can be especially effective when researchers use remote tracking techniques such as radiotelemetry or GPS (Armstrong et al. 2013). For small-bodied animals, active radiotelemetry is often the primary method because GPS technology has not been cost-effectively miniaturized and remote triangulation of frequencies locations can reduce location precision (Gottwald et al. 2019). When radiotelemetry data is combined with statistical movement modeling, researchers can effectively study movement and habitat use of reintroduced individuals (Cagnacci et al. 2010).

Robust movement analysis following data collection is critical to inform managers of how and where animals are spending their time. Spatially-explicit habitat suitability models provide maps of predicted suitable habitat and dynamic population models allow researchers to predict changing vital rates. However, behavior often varies across a cohort and these models lack the ability to fully incorporate individual variation. As a result, inferring management implications from these models can be challenging, as it can be unclear how to weigh conclusions from multiple models without knowing individual response. Agent-based models (ABMs) address these problems by introducing a spatially-explicit framework to quantify adaptive decisions of individuals and observing how patterns emerge throughout the system under a flexible set of variables (Dunning et al. 1995; Albeke et al. 2015). ABMs explicitly incorporate individual variability in behavior and have thus proven effective for studying animal movement (Railsback and Grimm 2005). Furthermore, understanding animal movement through

the lens of individual decision making can enhance our ability to detect patterns that may improve management decisions. For example, a study on amphibian populations in a dynamic floodplain system demonstrates this utility by incorporating spatially interactive subsystems to simulate changes in climate and weather on hydrodynamics affected site selection and population dynamics of the moor frog (*Rana arvalis*) (Dick and Ayllon 2017). This model includes non-migratory dispersal behaviors that many pond-breeding amphibians rely on to maintain viable metapopulations. In the context of management, using ABMs to understand these behaviors can be critical to the success of future reintroductions of amphibian species.

Captive-rearing and reintroduction have been utilized to support populations of the Gopher Frog (*Rana capito*), which is a medium-sized Ranid frog (adult SVL ~2.5 – 3.5 in.) (Jensen 2008, Terrell and Maerz 2016). This species has experienced declines due to habitat loss and degradation across its native range in the southeastern United States, where it occupies long leaf pine (*Pinus palustris*) savannas, flatwoods, and sand hills habitat in the Atlantic coastal plain (Jensen et al. 2008). It is listed as a species of special concern in all states in which it occurs (Georgia Department of Natural Resources 2015; Florida Fish and Wildlife Conservation Commission 2019; North Carolina Wildlife Resources Commission 2015; South Carolina Department of Natural Resources 2015; Alabama Department of Conservation and Natural Resources 2015) and is currently petitioned for listing on the Endangered Species Act (16 U.S.C. §§ 1531-1540 [1988]). Gopher Frogs breed in the winter months (Nov. – Mar.) in temporary, isolated wetlands that form near suitable upland habitat (Jensen et al. 2008). The Georgia Department of Natural Resources (GADNR) is in the process of restoring suitable breeding wetlands and surrounding upland habitat for gopher frogs and other target species. Reintroduction of juvenile gopher frogs complements management efforts for this species and

radio-tracking a subset of individuals during each release allows us to explore and analyze their movement.

Movement models informed by radio telemetry suggest that gopher frogs exhibit random dispersal with regards to direction of exit from a wetland and turning angles during movement (Hunt 2019). However, these models lack parameters that describe cohort survival and thus do not reveal the mechanistic patterns that can cause variability. Since dispersal is essential to population and metapopulation survival (Semlitsch 2008), characterizing patterns associated with juvenile dispersal and observing the decision making of individuals could be critical to informing future reintroduction efforts. Unlike adult frogs, which have been shown to exhibit site fidelity to refugia when migrating to and from breeding wetlands, juvenile amphibians are assumed to be naïve with respect to their new landscape (Rothermel 2004; Pittman et al. 2014). Additionally, non-breeding dispersal in many pond-breeding amphibians seems to occur primarily before individuals reach sexual maturity (Semlitsch 2008). Studies and field observations of reintroduced and wild-born juvenile gopher frogs suggest that survival of newly metamorphosed individuals is correlated with availability and use of underground refugia during dispersal (Roznik and Johnson 2009; Maerz et al. unpub. data). Gopher frogs have been observed using stump holes, small mammal burrows, and gopher tortoise (*Gopherus polyphemus*) burrows as primary refugia (Roznik and Johnson 2009; Humphries and Sisson 2012). These permanent refugia can provide protection from predators, a stable microclimate, and food (Jensen et al. 2008).

In gopher frogs, knowledge of terrestrial movement patterns and refugia use of juveniles is incomplete (Roznik and Johnson 2009a; Roznik and Johnson 2009b; Hunt 2019) and due to low detection and logistical constraints, it is difficult to measure how a juvenile frog perceives

the landscape. Results from an agent-based model suggest that environmental conditions such as weather, spatial distribution of gopher tortoise burrows, and groundcover affect juvenile survival and settlement (Burrow et al. 2023). However, this model uses linear movement and does not parameterize turning angles or step-length distances to individuals. To gain a complete picture of juvenile frog movement and inform management, a need exists to understand daily movement and predict space use. Here, we use radiotelemetry and ABM to conceptualize and observe patterns of juvenile gopher frogs that are associated with movement and availability and spatial arrangement of refugia. Our main goal is to accurately parameterize an ABM that describes juvenile gopher frog movement over the 4 days of dispersal following reintroduction. To do this we have the following objectives: 1) compare the model to patterns observed in real life and 2) conduct a sensitivity analysis to test which parameters have the most control over emerging patterns. The model will further our understanding of juvenile dispersal and improve our ability to design and implement reintroduction programs that maximize survival for gopher frogs.

## **Methods**

### *Study Site*

Reintroduction and radiotelemetry were conducted with juvenile Carolina gopher frogs in 2018 and 2019 at Sandhills Wildlife Management Area (SWMA) – East Tract in Taylor County, Georgia, USA, in 2021 at Alapaha River WMA (ARWMA) in Irwin county, Georgia, USA, and in 2022 at Townsend WMA (TWMA) McIntosh county, Georgia USA. All properties contain temporary, isolated, herbaceous wetlands with healthy gopher tortoise populations. Because of this, both ARWMA and SWMA currently sustain a breeding population of gopher frogs while

TWMA has historical records of gopher frogs. Additionally, the management plans for the sites explicitly target wetland management and maintaining suitable habitat for gopher frogs.

Sandhills WMA – East Tract is a 1,576 acre property located near Macon, Georgia (Figure 1). The site was historically managed for timber production, but since acquisition by the Georgia Department of Natural Resources (GADNR), it has undergone thinning, mulching, and is treated with prescribed fire to maintain the planted long leaf pine (*Pinus palustris*) overstory and wiregrass (*Aristida stricta*) dominated groundcover. Scrub-oak habitat mosaics the long leaf pine and wiregrass sandhills regime. Sandhills WMA-East Tract contains two natural ephemeral wetlands, one of which currently supports breeding for an apparently declining population of gopher frogs. It supports a healthy population of gopher tortoises (*Gopherus polyphemus*).

Alapaha River WMA is a 6,870 acre property located near Tifton, Georgia (Figure 1). It is almost six times the size of Sandhills WMA – East Tract and contains a variety of habitats including approximately 4,726 acres of upland pine forest and 2,143 acres of bottomland hardwood forest. The upland pine forest areas predominantly include planted loblolly (*Pinus taeda*) and slash pine (*Pinus elliottii*) stands that are currently undergoing treatments of thinning and prescribed fire. Sand hills dominated by wiregrass and scrub-oak habitat are scattered throughout the property. Alapaha River WMA contains approximately 50 wetlands of various sizes, vegetation regimes, and hydroperiods. Carolina gopher frogs have been sparsely documented at four wetlands and are thought to be in decline. It supports a healthy population of gopher tortoises in pine flatwoods and sand hills habitats.

Townsend WMA is comprised of four tracts of land totaling 32,000 acres on the north side of the Altamaha River. It contains a variety of forest habitats including upland forest and bottomland hardwood forest. The upland forest predominately includes loblolly and slash pine,

scrub-oak sandhills and mixed flatwoods. Wiregrass is one of the dominate groundcover plants in the upland habitat. The bottomland habitat is dominated by cypress (*Taxodium spp.*), hickories (*Carya spp.*), and water tupelo (*Nyssa aquatica*). There are many isolated wetlands scattered through the sandhills and upland areas. This habitat also supports a healthy population of gopher tortoises and other sandhills specialists like the eastern diamondback rattlesnake (*Crotalus adamanteus*) and eastern indigo snake (*Drymarchon couperi*). This property has historically supported breeding populations of gopher frogs with the last documented record occurring approximately 30 years ago.

#### *Data Collection*

In 2018, 2019, 2021, and 2022 we captive reared Carolina gopher frog eggs to metamorphosis at the University of Georgia and the United States Fish and Wildlife National Fish Hatchery in Warm Springs, Georgia. The gopher frog eggs were collected from the Savannah River Site in Aiken, South Carolina in 2018, SWMA in 2019 and 2022, and ARWMA in 2021. We released 45 frogs at SWMA in 2018, 29 frogs at SWMA in 2019, 27 frogs at ARWMA in 2021. In 2018 and 2019, we fit each frog with radio transmitters that attached via external belts like the method described by Muths 2003. The belts were constructed of elastic bracelet material connected to veterinary suture material that was threaded through the transmitter. The dissolvable suture material ensures that the belt would fall off after approximately 60 days. In 2018, 2019 and 2021, we used Holohil LB-2X transmitters (approx. weight 0.27 grams) and in 2022, we used Advanced Telemetry Systems T15 Tiny Transmitter (approx. weight 0.15 grams) because of a reported higher durability and longer battery life. We weighed pre-release to adhere to the standard that the weight of the transmitters did not exceed

10% of the individuals body mass (White and Garrott 1990). These methods were approved and conducted under University of Georgia Animal Care and Use Protocols A2018 02-019-Y2-A6 and A2021 02-010-Y3-A2.

Following release, we attempted to radio-track each frog at least 3 times per night. These were not fixed tracking intervals. The exact number of locations we gathered per individual per night depended on the number of active individuals with transmitters, weather conditions, and other logistical factors. Our modelling and analysis depend on only a daily location, but consistently following each frog throughout the night ensures a better of understanding of habitat use and makes it easier find frogs that moved greater distances. To locate individuals, we used a 3-element handheld Yagi-type antenna and we recorded each location using GPS. We visually located all individuals to the best of our ability. In rare instances where dense cover made it impossible to visually locate the frog, we used triangulation to get an approximate location. If we suspected a frog found an underground refuge (i.e., gopher tortoise burrow), we used a gopher tortoise burrow camera to check the burrow for that individual. During each relocation we measured temperature, humidity, and windspeed. We recorded refugia use and refugia type.

### *Model Overview*

To accurately describe and simulate juvenile gopher frog movement, we used our telemetry data from SWMA and ARWMA to parameterize an agent-based model in Netlogo (Wilensky 1999). We did not include telemetry data from TWMA because we did not obtain sufficient data for each individual due to a few frogs finding burrows in less than 24 hours or more commonly, quick mortality. Prior to data analysis, we binned the data into 24-hour intervals to ensure adequate detection for each individual. This also makes sense because our data indicates that

juvenile gopher frogs make nearly all of their movements at night, so daily movements are sufficient for the model. To parameterize daily movements, we used the step-length and turning angles from the first four nights of dispersal (Figure 2.2 and 2.3). We chose to pool data from SWMA and ARWMA to obtain a larger dataset and because this model does not apply to any specific landscape. We were limited to four nights because many transmitter signals were lost after 4 days either due to predation or unknown circumstances. Further description on model design, initialization and parameters is included in the following sections.

### *Model Landscape*

To accurately describe and simulate gopher frog movement, we designed a 169 ha model landscape containing a release point and randomly positioned refugia (gopher tortoise burrows). The model's spatial extent is a square of 1300 x 1300 square cells, each 1m x 1m in size. The total area is equal to 169 hectares. This landscape size was chosen to ensure that frog movement would not be spatially bounded during model testing. The fine resolution of grid cells was chosen for two reasons: (1) so the model can accurately represent the scale at which frogs move across the landscape and (2) so distribution of gopher tortoise burrows can be represented at the correct scale. The majority of habitat surrounding the wetlands at both sites is suitable for gopher tortoises. Therefore, the model randomly places gopher tortoise burrows on the landscape. We counted the number of burrows within a 1300m x 1300m square around the release points at ARWMA and SWMA to obtain an accurate range (250 – 350) for the number of burrows.

### *Model Parameterization*

There are five parameters that control the behavior of individuals in the model. We used the ‘adehabitatLT’ package (Calenge 2006) in R to generate movement statistics including daily step-length and turn-angle from the telemetry data (R core team 2022). We then fit distribution curves to step-length and turn-angle using the ‘fitdistrplus’ package (Delignette-Muller and Dutang 2015) in R. We created the following additional parameters to include in the model:

Daily survival ( $S_{\text{day}}$ ) – The probability of an individual surviving each day ( $S_{\text{day1}}$ ,  $S_{\text{day2}}$ ,  $S_{\text{day3}}$ ,  $S_{\text{day4}}$ ). We calculated this by counting the number of individuals that survived through four days and then divided that by the totally number of individuals released to obtain a four-day total survival ( $S_{\text{total}}$ ) probability. We then calculated the constant daily survival value that would result in the four-day total survival probability.

$$S_{\text{day1}} \times S_{\text{day2}} \times S_{\text{day3}} \times S_{\text{day4}} = S_{\text{total}}$$

$$S_{\text{total}} = 0.54$$

Probability of stopping ( $P_{\text{stop}}$ ) – The probability that a frog permanently stops at a burrow if there is a burrow in the vicinity of the frog. Our telemetry data indicates that gopher frogs do not move significant distance after settling in a gopher tortoise burrow. Therefore,  $P_{\text{stop}} = 1.0$ .

Probability of movement ( $P_{\text{move}}$ ) – The probability of a frog moving on any given day. We estimated this value from our telemetry data using a generalized linear model. We included this parameter to help account for environmental variation, behavioral variation, and use of non-permanent refugia. The estimated value was  $P_{\text{move}} = 0.85$ .

### *Model Initialization*

Figure 2.4. describes the overall model process. The model is initiated with 500 individuals placed at the same central point. 500 frogs were chosen because that was the number released in each of the field seasons (2018, 2019, & 2021), and is a reasonable number to release in the current rearing program. When each frog is created, it's nightly movement distances are randomly selected from a nightly gamma distribution that represent observed movements pooled from radio-tracked individuals. Simultaneously, a pre-determined number of gopher tortoise burrows are placed on the landscape. There are no individual variables assigned to burrows. Secondly, the frogs make their nightly movements. Because we typically release frogs at the edge of a wetland, and there is no space in the model representing a wetland, their initial heading is determined from a random draw from 0 – 360. The initial heading decision promotes simplicity and prevents bias regarding the spatial arrangement of the burrows. Subsequent headings are determined by drawing from normal turn angle distributions representing data collected on radio-tracked individuals. When a heading is determined, a frog moves 1 step (m) at a time until it either reaches its predetermined movement distance or encounters a burrow. After each frog has completed its nightly movement (or stopped at a burrow), the next nightly movement begins. Finally, distance moved, a burrow-found binary parameter, and [other variables] are reported for each frog and written to output files after each nightly movement.

### *Model Fitting*

It was critical to adjust the model so that it reflects observed patterns of gopher frog dispersal. To do this, we created a parameter called 'frog-radius', which represents the area around a frog in which it can detect a gopher tortoise burrow. We started with a 'frog-radius' of 1 (meters) and

tested each value up until 5. We repeated each simulation 10 times and extracted the net displacement distances for each frog. We used a Kolmogorov-Smirnov (K-S) test to compare the distributions of net displacements in each simulation to the distribution of net displacements from the telemetry data. The model simulations were conducted in Netlogo (Wilensky 1999) and the analysis was conducted in Program R 4.1.1 (R Core Team 2022).

### *Sensitivity Analysis*

We performed a sensitivity analysis to assess the relative importance of each parameter to the net displacement of the frogs. Additionally, many of our parameters were based on expert opinion, so a sensitivity analysis is critical to assessing the legitimacy of our assumptions in a biological context. In our analysis, we assessed the following parameters: step-length, daily survival, probability of stopping, number of burrows, turn angle, probability of movement, and burrow survival. For all parameters with a single input value (e.g., daily survival, burrow survival, number of burrows, probability of stopping, probability of movement), we directly adjusted the value by  $\pm 10\%$ . Because values for step-length and turn angle were drawn from distributions, we adjusted the means of those distributions by  $\pm 10\%$ . We ran the model 25 times for each parameter adjustment, saved the mean net displacement per run, and then averaged all the runs. The sensitivity analysis was performed in Netlogo (Wilensky 1999) and R (R Core Team 2022).

## Results

### *Model fitting by Comparison to Observed Patterns*

We were able to fit the model to the observed distribution of net-displacements by adjusting the ‘frog-radius’ parameter. The test compared the resulting distributions of net displacements (Figure 2.5). Table 2.1 shows the resulting p-values associated with each ‘frog-radius’ value vs. the observed scenario. The observed values vs. the 1m radius was the only scenario where the difference between the two distributions was non-significant (Table 2.1.,  $p > 0.05$ ).

The observed range of net displacement values was 7.73 – 448.01 meters while the range across all simulations was 2.00 – 755.00 meters (Table 2.1). The mean net displacement of all simulations had a range of 133.88 – 159.93 meters and the mean of the observed net displacements was 178.41 meters (Table 2.1).

### *Sensitivity Analysis*

Net-displacement was most sensitive to daily step-length and probability of movement (Figure 2.6). The parameter that caused the least change in net-displacement was burrow-survival (Figure 2.6). Daily survival and number of burrows both induced a moderate response in both directions while probability of stopping and turning angle both exhibited moderate responses in only one direction (-) due to their initial value being 1 (Figure 2.6). It should be noted that the sensitivity of net displacement to daily survival seemed to be slightly stronger with a negative change (Figure 2.6).

## Discussion

Gopher frog populations are likely dependent upon juvenile dispersal to maintain persistence on the landscape. However, juveniles are difficult to detect in the wild (Roznik and Johnson 2009). Reintroduction efforts can help population persistence by augmenting the number of individuals and boosting survival, but the effectiveness of these efforts can be diminished by poor release decisions or lack of understanding about post-release behavior. The literature lacks robust models that describe the dispersal of juvenile gopher frogs. We used radio-telemetry data and expert opinion to construct an ABM that fills this knowledge gap. Our model goes a step beyond a random-walk model and incorporates individual behavior to accurately simulate juvenile gopher frog dispersal. Thus, we add to the list of tools to help a species in decline through most of its historic range.

Landscape naïveté (Semlitsch 2008), low detection rates (Roznik and Johnson 2009), and a lack of research on sensory cues of juvenile gopher frogs make it difficult to empirically model dispersal behavior and its drivers. Burrow et al. 2023 help resolve this problem by predicting fine scale dispersal movements under two microhabitat selection scenarios. They determined that availability of gopher tortoise burrows and a wetter weather regime had the most positive effect on frog survival regardless of microhabitat selection. We modelled nightly juvenile gopher frog movements to predict net-displacement distances and incorporated random, non-mechanistic parameters (e.g., probability of movement, daily survival, frog-radius) to capture variation modelled at a finer movement scale by Burrow et al. 2023. That model uses rate-based hourly movements to predict total distance movement away from the wetland across 12 days. They predicted realistic movement distances of up to 300.5 meters from the wetland. This maximum differs from our model, where some frogs moved up to 600 meters in only 4 days (Figure 2.2). In

addition, our field observations indicate much larger distances are possible. Given that we successfully fit our model to observed net displacement distances by comparing the distributions of simulated net displacements vs. observed net displacements, we can make a reasonable assumption that these distances are realistic. Both models use a 1m<sup>2</sup> patch size to model frog movement, but the rate-based movement in Burrow et al. 2023 may account for the difference in net-displacement distances. Our model lacks the ability to predict microhabitat selection and influence on fine scale habitat factors and the Burrow et al. 2023 model is limited by linear movement and lack of turning angles. Therefore, these two models complement one another in terms of predicting juvenile gopher frog dispersal patterns at different scales and demonstrate the effectiveness of ABMs for studying this system.

Gopher tortoise burrows are an important factor when considering juvenile gopher frog survival. In most of their range, they rely on gopher tortoise burrows as refugia critical to survival when conditions on the surface are inhospitable. Furthermore, models and field studies found that availability of gopher tortoise burrows affects survival (Roznik and Johnson 2009; Hunt 2019; Burrow et al. 2023). We included gopher tortoise burrows in our model because of their importance to gopher frog ecology, but we don't have a complete understanding of the role that they play in juvenile dispersal. Our sensitivity analysis showed that net-displacement was sensitive to the number of burrows on the landscape. This provides some evidence that gopher tortoise burrows play a role in juvenile dispersal patterns beyond survival. Furthermore, we fit the model to a parameter that attempts to explain the role of burrow detection in dispersal. The 1m frog-radius was the only value that fit to our observed data, however, there is still a visual gap between empirical cumulative distribution function (ECDF) curves (Figure 2.3). We believe this occurs for two reasons. First, the observed distributions are formed from far less data than

those from model simulations. This accounts for the jaggedness of the observed curve. Secondly, the movement parameters (turning angle and step-length) come from telemetry data conducted on landscapes where burrows were not randomly placed, as they were in our model.

Additionally, Gopher frog distribution on the landscape aligns with distribution of gopher tortoise burrows (Marshall et al. 2023). Therefore, the gap in the ECDF function between our 1m frog radius scenario and observed data may result from the non-random distribution of burrows in real landscapes. Because there is evidence to suggest that finding a burrow boosts the survival probability of an individual, understanding the ability to find a burrow and role of the number of burrows is important to determining success of reintroduced individuals on the landscape.

Understanding the sensitivity of the model parameters is critical to making inferences about the model results. It's not surprising that net displacement was most sensitive to step-length, because both are distance metrics. However, net displacement was almost just as sensitive to probability of movement. This likely means that this parameter is successful at capturing some of the movement variation due to habitat, weather, or other conditions affecting movement that are not explicitly defined in the model. While not as sensitive, daily survival and probability of stopping also likely capture behavioral variation caused by external factors. Net displacement was not quite as sensitive to the number of burrows, the degree of sensitivity it does show supports the idea that gopher tortoise burrows are an essential resource to juvenile gopher frogs. The survival in a gopher tortoise burrow had little to no effect on net displacement, which is not surprising because the frogs aren't moving once they've settled in a burrow. The last movement parameter, turning angle, showed some sensitivity to a higher turning angle, but no sensitivity to lower turning angles. We don't often observe juvenile gopher frogs making drastic changes in direction relative to their distance traveled, so turn angle likely has little effect

on net displacement. However, this model does not impose any changes to turning angle when an individual encounters unsuitable habitat.

We chose to combine the data from both sites to build a single, more robust model with more input data. One reason for this is that it allowed us to parameterize the model on a generic landscape and randomize the locations of gopher tortoise burrows. Furthermore, the size difference between the two WMAs is a negligible difference in terms of radiotelemetry due to the scale at which juvenile Gopher frogs dispersed. However, acreage and property extent matter in a management context, where frogs may have the ability to disperse off-property (Hunt 2019). The difference in number of wetlands may have site-level metapopulation consequences, but this work does not target those questions. It is unclear whether differences in the habitat surrounding each sites respective wetlands are significant for juvenile movement, but because the probability of movement parameter has a high degree of sensitivity, we can assume that it captures some amount of unknown variation.

The advantage of incorporating parameters that account for variation that might be difficult to measure is that it allows us to apply the model to different scenarios where flexibility is crucial. For example, future reintroductions of gopher frogs may take place at different wetlands on the same properties or different properties altogether. Because we don't include site specific attributes yet include parameters in the model that allow for variation and flexibility, we can apply this ABM to future reintroduction sites to observe patterns of juvenile gopher frog dispersal before reintroduction takes place. Doing so will allow us to make more informed decisions on whether to release at a certain site, the exact release points, and how many individuals to release.

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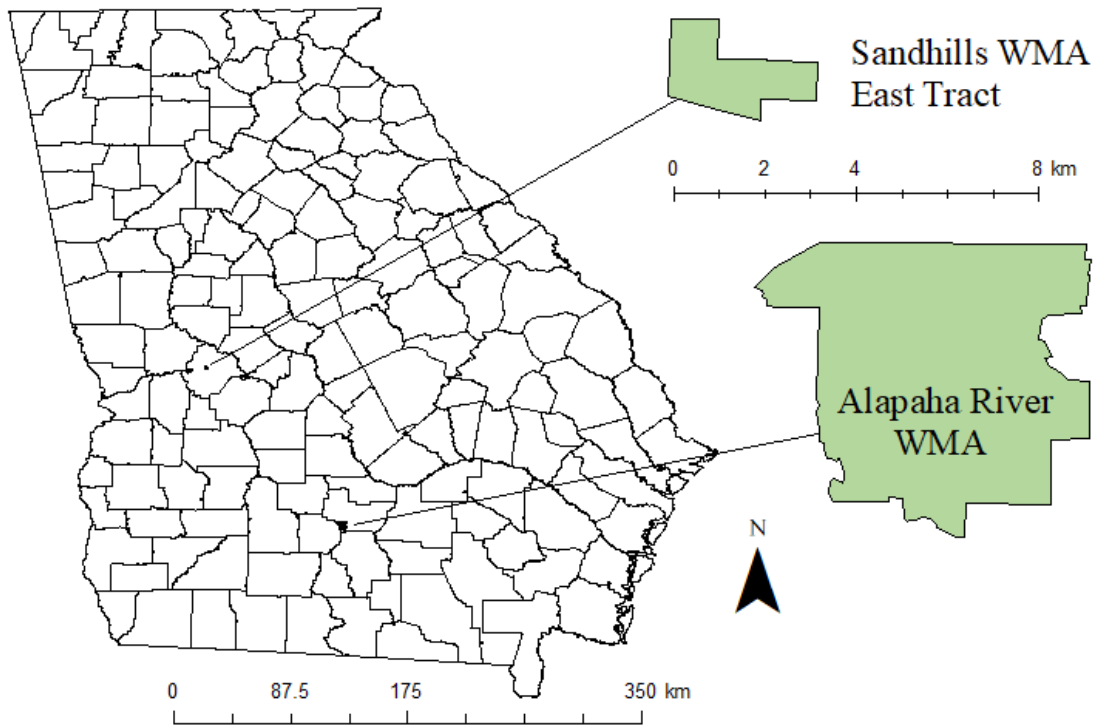


Figure 2.1. A map showing locations of Sandhills and Alapaha River WMAs. The property size shown is to relative scale.

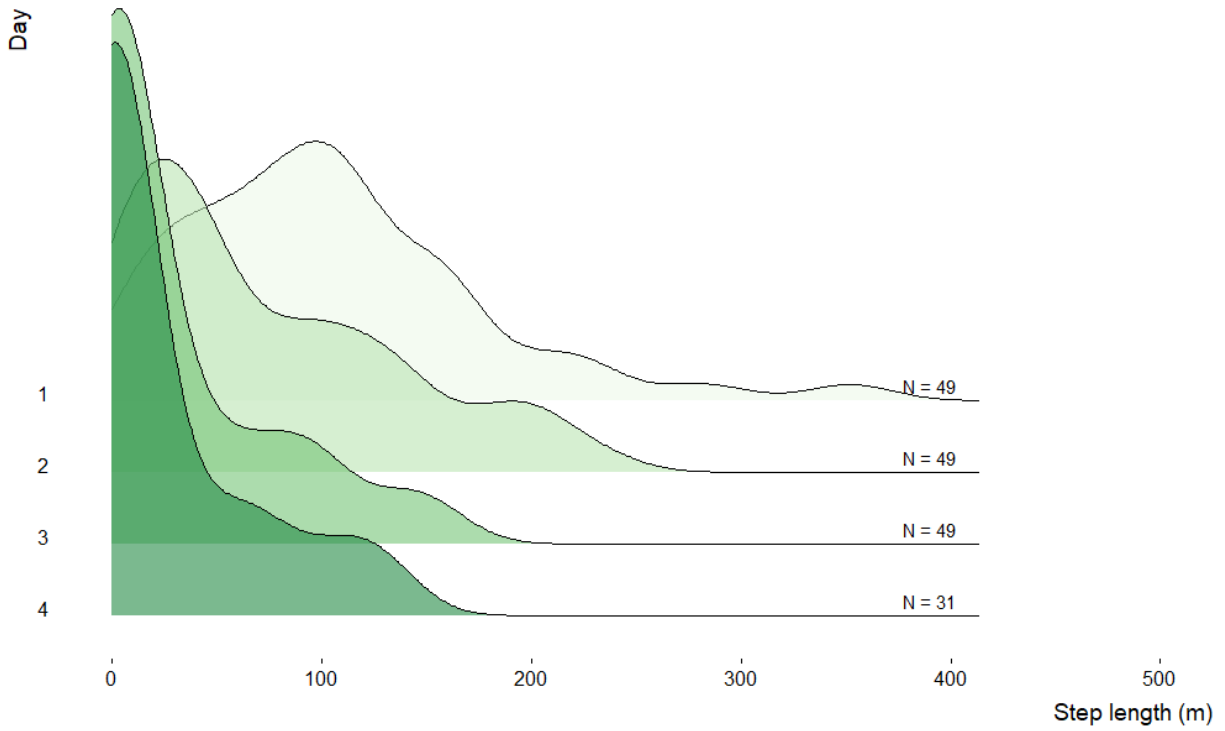


Figure 2.2. Frequency distribution of step lengths for the first four days of juvenile gopher frog dispersal.

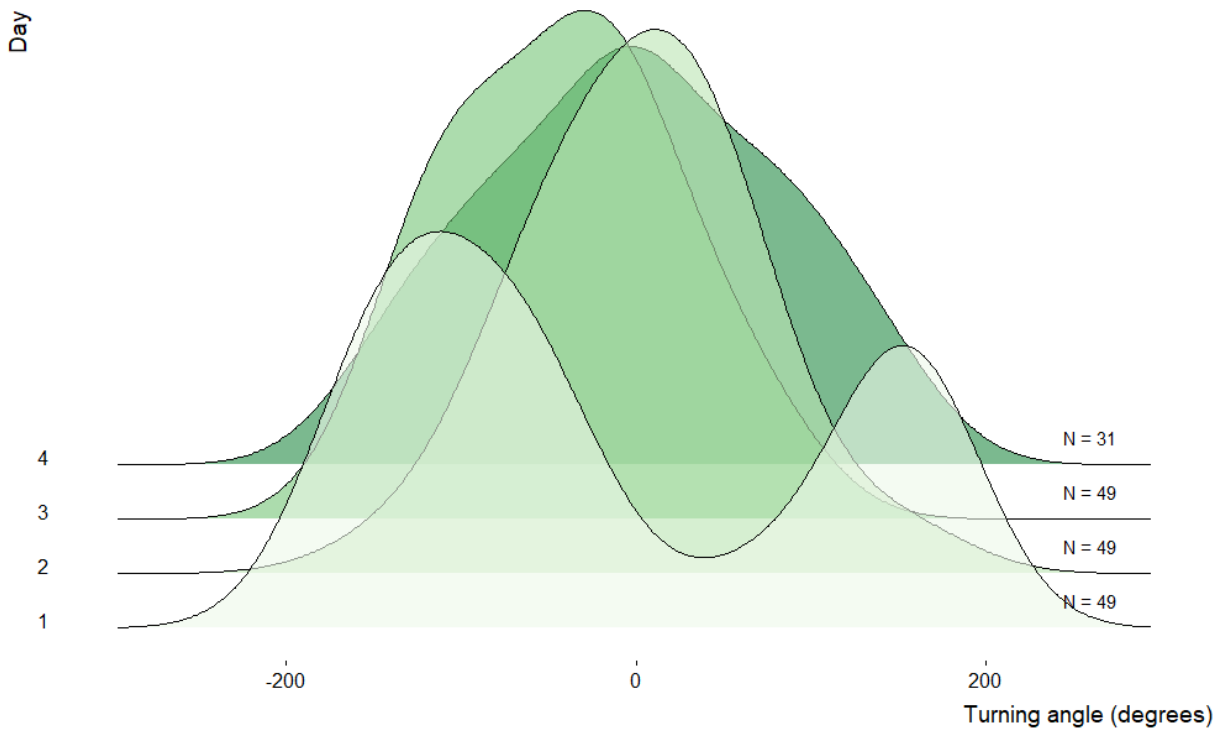


Figure 2.3. Frequency distribution of turn angles for the first four days of juvenile gopher frog dispersal.

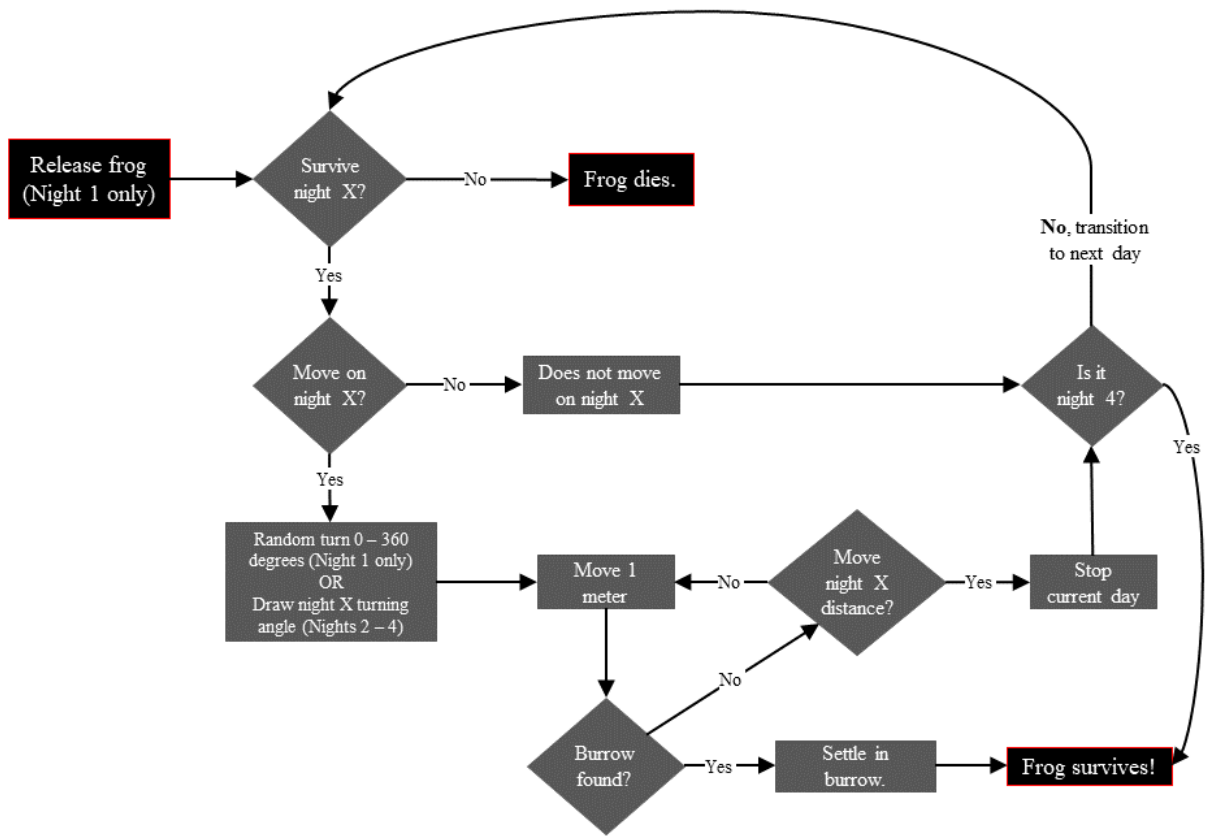


Figure 2.4. A flow chart describing the pathway of behaviors and decision making for an individual juvenile gopher frog in our ABM.

Table 2.1. A table showing the statistics of the observed net-displacement values and the statistics from the model fitting exercise using a ‘frog-radius’ of 1m, 2m, 3m, 4m, & 5m. The table also shows the resulting p-value from the K-S test which compared each simulated distribution of net-displacements to the observed distribution.

<b>Test scenario</b>	<b>Min. net displacement</b>	<b>Maximum net displacement</b>	<b>Mean net displacement</b>	<b>K-S test p-value</b>
Observed	7.73	448.01	178.41	N/A
Frog-radius 1m	2.00	642.31	159.93	0.13
Frog-radius 2m	4.00	755.00	151.9	0.047
Frog-radius 3m	2.00	583.00	151.8	0.043
Frog-radius 4m	3.00	673.00	144.86	0.008
Frog-radius 5m	2.00	676.00	133.88	0.0007

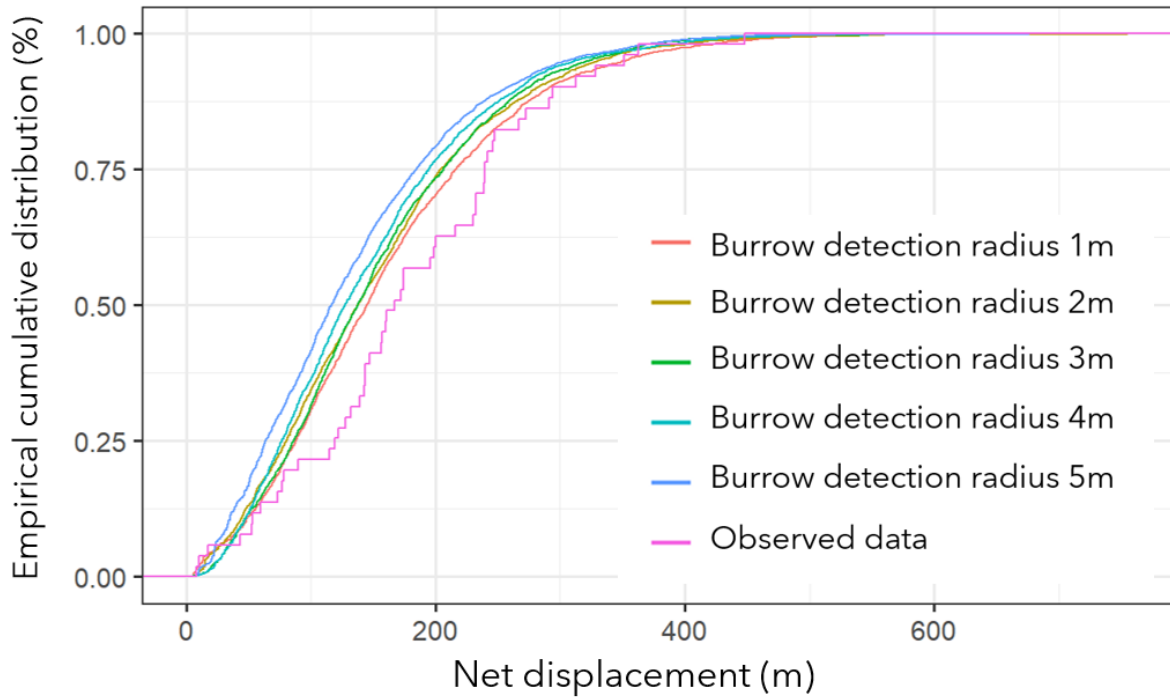


Figure 2.5. An empirical cumulative distribution plot showing the net displacement values for each simulation and observed from least to greatest against a percent scale. This shows the relative distances between values within each distribution.

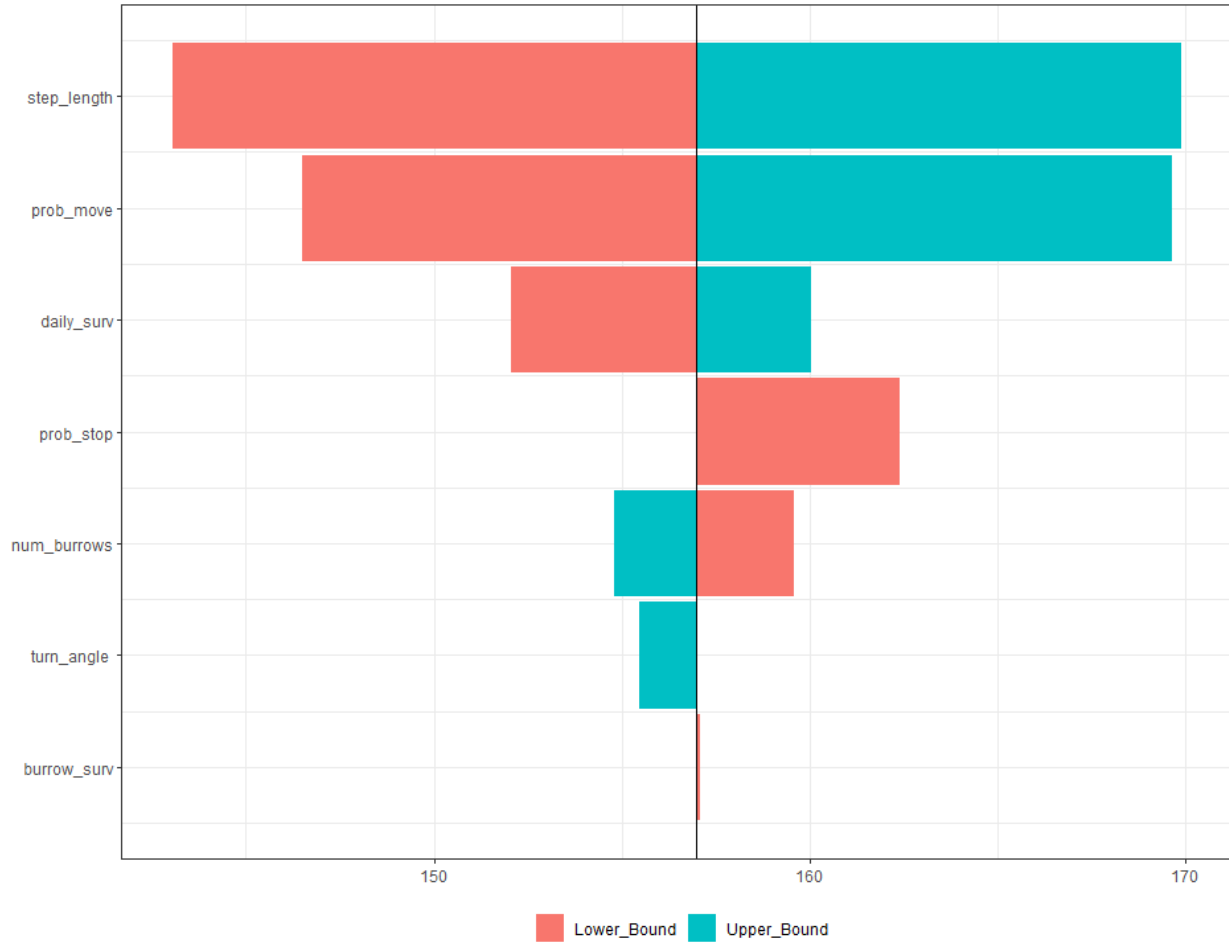


Figure 2.6. Diagram that shows the sensitivity of the change in net displacement to the model parameters. The vertical line represents the mean net-displacement of the fitted model. Each bar represents the parameters adjusted by  $\pm 10\%$ .

## CHAPTER 3

### INFORMING REINTRODUCTION OF JUVENILE GOPHER FROGS (*RANA CAPITO*) ON ALAPAHA RIVER WILDLIFE MANAGEMENT AREA BY SIMULATING DISPERSAL

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<sup>2</sup>Thesing, B. J., N.P. Nibbelink, N.P., J. C. Maerz and H.E. Gaya. 2023. To be submitted to *Southeastern Naturalist*.

## **Abstract**

The gopher frog (*Rana capito*) is listed as a Species of Greatest Conservation Need in all states in which it occurs and is currently petitioned to be listed under the Endangered Species Act. Efforts to conserve and manage this species at Alapaha River Wildlife Management Area have focused on wetland restoration, population monitoring, and captive-rearing for reintroduction. We used an agent-based juvenile gopher frog dispersal model to simulate reintroduction scenarios on the landscape and demonstrate the application of this tool for informing management decisions. We create density maps showing where most frogs disperse under different reintroduction scenarios. The inverse density map is then used as a cost surface to estimate relative connectivity between breeding wetlands and identify the priority areas for dispersing juvenile gopher frogs. Results inform both priority areas for land management as well as reintroduction schemes likely to best support metapopulation structure via juvenile dispersal.

## **Introduction**

Species reintroduction programs have proved to be a successful conservation tool for a variety of taxa (Seddon et al. 2014). Reintroduction is commonly used to reinforce declining populations or establish new populations through the translocation of individuals onto a novel yet presumed suitable landscape (Seddon et al. 2014). In some instances, reintroduction programs are coupled with restoration of degraded habitat to repopulate a declining species. However, reintroduction programs are resource intensive and effort should be given to maximize success and prevent failed attempts. Thus, understanding a species ability to persist on a restored landscape prior to reintroduction is critical to the success of these programs.

Species persistence on the landscape depends on its ability to survive, disperse, and reproduce. Many species rely on complementary habitats in which different habits are used at different times by the same group of species during a set period of time (Mandelik et al. 2012). Therefore, one specific habitat cannot support long-term population survival, but a mosaic of areas providing different resources is most optimal (Wann et al. 2020; Rothermel and Semlitsch 2006; Daily et al. 2001). For example, many amphibians exhibiting a biphasic life history spend the non-breeding season in upland refugia and migrate to wetlands to reproduce (Semlitsch 2008). While each habitat is essential, neither can successfully maintain persistence of the species on the landscape without the other. When breeding events occur, newly metamorphosed juveniles leave the wetland and disperse onto the landscape. Furthermore, amphibian movement occurs at different scales (Bailey and Muths 2019). Adults show relatively high levels of site fidelity with regards to their breeding wetlands (Semlitsch 2008) and therefore consequences of this type of movement are restricted to a population whereas juvenile dispersal has consequences to the metapopulation (Bailey and Muths 2019). Because juveniles show the ability to move great distances when they leave the wetland, promotion of new site colonization and maintaining metapopulation connectivity likely falls upon juvenile dispersal. Maintaining metapopulation connectivity is important because low levels of population synchrony often exist in pond-breeding amphibians (Cayuela et al. 2020) and both natural or anthropogenic changes to the habitat can influence populations differently. Thus, efforts to understand juvenile dispersal in pond-breeding amphibians where scale influences how we think about conserving individuals, the population, and the metapopulation can help improve and prioritize management decisions.

The gopher frog (*Rana capito*) is a pond-breeding species that relies on complementary habitats. A medium-sized ranid frog (approx. adult SVL 2.5 – 3.5 in.), it occupies long leaf pine

(*Pinus palustris*), flatwoods, and sand hills habitat in the Atlantic coastal plain (Jensen et al. 2008, Terrell and Maerz 2016). In these habitats, it relies on gopher tortoise (*Gopherus polyphemus*) burrows, small mammal burrows, and stump holes in the upland to provide a stable microclimate and protection from predators during the summer months (approx. April. – October). In the winter months (approx. November. – March.), it migrates from upland refugia to temporary, isolated wetlands to breed. After metamorphosis, juveniles disperse to the upland where survival depends heavily upon their ability to find underground refugia (Roznik et al. 2009; Roznik and Johnson 2009a; Roznik and Johnson 2009b). Due to habitat loss and degradation across its native range in the southeastern United States, it is listed as a species of greatest conservation need in all states in which it occurs (Georgia Department of Natural Resources 2015; Florida Fish and Wildlife Conservation Commission 2019; North Carolina Wildlife Resources Commission 2015; South Carolina Department of Natural Resources 2015; Alabama Department of Conservation and Natural Resources 2015) and is currently petitioned for listing on the Endangered Species Act (16 U.S.C. §§ 1531-1540 [1988]).

The Georgia Department of Natural Resources (GADNR) is in the process of restoring suitable breeding wetlands and the surrounding upland habitat for gopher frogs and other target species at Alapaha River Wildlife Management Area (ARWMA). Concurrently, reintroduction efforts are underway to bolster the current population of gopher frogs that we suspect is in decline (Terrell and Maerz 2016). The property contains isolated wetlands, many of which are scattered throughout upland habitat that is suitable for gopher frogs. Reintroduction efforts have targeted the release of captive-reared frogs to take place at two wetlands thus far, one which has had documented breeding of gopher frogs (e.g., 1 egg mass in 2021) and one which has highly suitable upland habitat. However, we have been unable to measure the success of these actions

due the difficulty of monitoring juvenile amphibians and the length of time (18 – 24 months) it takes gopher frogs to reach sexual maturity and show signs of breeding. Therefore, it is important to understand how gopher frogs will disperse on the landscape post-reintroduction to maximize the success of captive-rearing and release efforts in terms of establishing long-term metapopulation persistence.

Researchers often employ predictive models to assess the impact of numerous conservation scenarios on a species prior to decision making (Runge et al. 2014; Sandford et al. 2017; Scroggie et al. 2019; Wightman et al. 2022; Gaya et al. 2023). Agent-based models (ABMs) have proved effective for this task because they explicitly incorporate individual variability in behavior and thus allow researchers to predict species interactions with the landscape (Railsback and Grimm 2005). Furthermore, ABMs have been used to explore how amphibians respond to changes in environmental factors and inform management decisions (Burrow and Maerz 2022; Burrow et al. 2021; Allen et al. 2020; Westervelt et al. 2013; Rustigian et al. 2003). One of these studies (e.g., Burrow et al. 2021) looked at how gopher frog survival and dispersal are affected by weather conditions, ground cover, and other environmental factors. While this is critical to informing how management efforts target specific habitat variables such as ground cover and refuge availability, the need exists for a model to predict landscape connectivity at a broader scale. Therefore, our objective for this project was to use an ABM to predict landscape connectivity for gopher frogs on ARWMA by simulating different reintroduction scenarios. We are testing the hypothesis that varying reintroduction scenarios by changing the number of frogs released, target wetlands, and which side of the wetland to conduct releases will influence total landscape connectivity. The result of these simulations will help

guide management actions on ARWMA by determining specific areas that are most important to maximizing landscape connectivity for gopher frogs.

## Methods

### *Study Site*

We simulated juvenile gopher frog dispersal at Alapaha River Wildlife Management Area in Irwin County, Georgia, USA. ARWMA is a 6,870 acre property located near Tifton, Georgia (Figure 3.1). It contains a variety of habitats including approximately 4,726 acres of upland pine forest and 2,143 acres of bottomland hardwood forest. The upland pine forest areas predominantly include planted loblolly (*Pinus taeda*) and slash pine (*Pinus elliottii*) stands that are currently undergoing treatments of thinning and prescribed fire. Sand hills dominated by wiregrass and scrub-oak habitat are scattered throughout the property. Alapaha River WMA contains approximately 50 wetlands of various sizes, vegetation regimes, and hydroperiods. Carolina gopher frogs have been sparsely documented at four wetlands and are thought to be in decline. It supports a healthy population of gopher tortoises in pine flatwoods and sand hills habitats. Additionally, the management plan explicitly targets wetland management and maintaining suitable habitat for gopher frogs.

### *Model Overview*

To simulate juvenile gopher frog dispersal on ARWMA, we applied the juvenile gopher frog agent-based movement model from Chapter 2 of this thesis to the landscape. This model uses telemetry data to parameterize the movement of reintroduced juvenile gopher frogs for the first four nights of dispersal. The simulated frogs stop at gopher tortoise burrows if they find one. Additionally, it includes a daily survival rate and daily probability of movement. Here, we apply

that movement model to multiple release points on the landscape to simulate different reintroduction scenarios. We built this simulation in Netlogo (Wilensky 1999).

### *Model Landscape*

The model landscape consists of the ARWMA boundary, priority wetlands, and gopher tortoise burrows (Figure 3.2). We did not include any fine scale habitat factors (e.g., humidity, groundcover, temperature) because the movement model has built-in parameters (i.e., observed probability of movement) to account for some of that variation. For wetlands, we selected five priority wetlands that are the main target sites for gopher frog reintroduction at ARWMA. We consider these wetlands target sites because each possesses a combination of having previous breeding or calling documented, highly suitable surrounding upland habitat, or are deemed suitable for breeding. The wetland and boundary data were merged into a single raster dataset to easily incorporate with the Netlogo patch-defined landscape. For gopher tortoise burrow locations, we obtained line transect distance sampling survey (LTDS) data from GADNR. Because we needed a complete map of burrows for the movement model to perform accurately, we used canopy cover, soil, and locations of historic agricultural fields to model suitable habitat for gopher tortoises on the landscape using MaxEnt (Phillips et al. 2004, 2006) and input the resulting habitat suitability layer  $\mathbf{X}$  into a spatially explicit distance sampling model (Miller et al. 2013; Wilson et al. 2021) to estimate gopher tortoise burrow densities. Spatially-explicit distance sampling allows for inference on the effect of land type on abundance, while accounting for imperfect detection of individuals (Miller et al. 2013). We modeled gopher tortoise burrow abundance ( $N$ ) and location through an inhomogeneous Poisson point process:

$$E(N) = \int \mu(\mathbf{s}) d\mathbf{s}$$

Where the intensity surface,  $\mu(\mathbf{s})$ , is modeled as a function of habitat suitability  $\mathbf{X}$  at each location in the study area:

$$\log(\mu(\mathbf{s})) = \beta_0 + \beta_1\mathbf{X}$$

The probability density of a burrow at any given location,  $s_i$  is calculated as the intensity at that location divided by the expected number of burrows in the study area:

$$p(s_i) = \frac{\mu(s_i)}{E(N)}$$

To model the locations of potentially missed burrows, we used a data-augmentation technique (Royle and Dorazio 2008), where the known distances for  $n_{ind}$  found burrows were augmented with a large number  $n_A$  of unknown values representing potentially missed burrows. Assuming transect lines were placed independently with respect to the burrows, we drew distances ( $x_i$ ) for augmented burrows from a uniform distribution such that:

$$x_i \sim \text{Uniform}(0, Bx)$$

where  $Bx$  represents a fixed maximum distance that a burrow could be detected from the transect line. In our analyses, we fixed  $Bx$  at 25m, consistent with LTDS guidelines for gopher tortoises (Smith et al. 2016). Burrows were included in the population with probability  $\psi$ :

$$w_i \sim \text{Binomial}(1, \psi).$$

$$\psi = \frac{E(N)}{n_{ind} + n_A}$$

All real burrows, both drawn from the augmented population plus those found during the survey, were then summed into a total population  $N$  which was used to find the total population of burrows:

$$N = n_{ind} + \sum_{i=1}^{n_A} w_i .$$

Using the half-normal detection function, we modeled probability of detection of burrow  $i$  at distance  $x$  from the transect line as:

$$g(x) = e^{\left(\frac{-x_i^2}{2\sigma_i^2}\right)},$$

With detection parameter  $\sigma$  drawn from a vague uniform prior. The output of predicted burrow locations was rendered and loaded into the Netlogo framework.

### *Model Initialization*

The model begins by setting up the landscape and placing frogs at release points that are determined by the model scenario (Table 3.1). The number of frogs placed at each release point is also dependent on the scenario. When the model is run, frogs disperse from each release point by making nightly movements parameterized by telemetry data (Thesing, Chapter 2). Unlike the generic model (Thesing, Chapter 2), which had no restrictions on frog movement, this model did not allow frogs to reenter wetlands, and instead applied a 180 degree turn if a wetland edge was encountered. We parameterized the model this way because observed telemetry paths indicate that juvenile gopher frogs rarely disperse back into the wetland. Once dispersal is completed after four nights, the final locations are exported from Netlogo and used in our landscape connectivity analysis.

### *Reintroduction Scenarios*

The model operates under the assumption that we have approximately 2000 total juvenile gopher frogs to release each year due to the limitations of large-scale captive rearing. Historically, the goal has been to release 500 individuals at target wetlands each year. There are six wetlands that are suitable for releasing gopher frogs. We define these as our priority wetlands

because they are the subject of current management and monitoring efforts for gopher frogs and/or sustain a breeding population. In our reintroduction scenarios, we selected five of the six wetlands to reintroduce frogs. We left out wetland 31 from receiving frogs because of its proximity to wetland 30 to avoid redundancy (Figure 3.2). We chose five scenarios where we left out one of those wetlands and reintroduced frogs at the other four. We also changed the edge of the wetland chosen for release in some scenarios because our telemetry data indicates that frogs tend to orient themselves and move away from the wetland. Finally, we ran two scenarios where we reintroduced 1000 frogs at two wetlands instead of 500 at four wetlands. We selected this suite of scenarios to demonstrate a range of release efforts, rather than rigorously test every possible combination. Because our objective is to inform management, we developed reintroduction scenarios that were as realistic as possible while also highlighting differences in landscape connectivity. Table 3.1 describes which factors were changed in each scenario.

### *Landscape Connectivity Analysis*

To measure landscape connectivity for juvenile gopher frogs on ARWMA, we exported all final locations of frogs from each Netlogo scenario into ArcMap version 10.8 (ESRI, Redlands, CA). We used those layers to create a point density raster for each scenario where each cell value corresponds to the density of final frog locations within a 1000-meter diameter. Each raster layer has 10m x 10m resolution. We used the cost connectivity tool in ArcMap to estimate the least cost path between two nodes (wetlands) and creates a least cost network between all given nodes. Our landscape connectivity analysis operates under the assumption that if there are more frogs in an area, the easier it is to move on the landscape. Therefore, we took the inverse of the density raster (i.e., high density values correspond to lower resistance) and used that as the resistance

layer to create least-cost paths between the priority wetlands. We are comfortable with this assumption because the movement model was fit to observed data from radiotelemetry and contains parameters (e.g., probability of movement) that account for movement variation due to environmental variables. Furthermore, the generic movement model includes daily survival, which accurately simulates the number of gopher frogs that make it through 4 nights of movement. Our model allows for frogs to find and settle gopher tortoise burrows, enhancing the realism of dispersal simulations. If a gopher frog finds a permanent refuge (i.e., gopher tortoise burrow), they have a high likelihood of settling in that burrow. If we assume that frogs after 4 nights are likely to continue similar movement trends, we can comfortably say that our network of least cost paths between wetlands serves as a good proxy for potential movement corridors. We compare scenarios by reporting the total cost (sum) of each scenario, the average cost per path between wetlands for each scenario, and the range of costs for all paths between pairs of wetlands in each scenario. Finally, we use the Euclidean distance tool in ArcMap to generate hotspot areas surrounding each least cost path between wetlands to identify priority areas of gopher frog movement.

## **Results**

### *Gopher tortoise habitat and burrow estimation*

The Maxent model produced a suitable habitat layer for gopher tortoises on ARWMA (Figure 3.3). The model has an AUC of 79.6. The most important variable to modelling suitable gopher tortoise habitat on ARWMA was canopy cover (Figure 3.4).

The spatially-explicit distance sampling model predicted the density and distribution of 2000 burrows (95% C.I.;  $1480 < x < 2578$ ) across the suitability landscape. The final burrow map we used in our ABM includes the real burrow locations from the transect data (Figure 3.3).

### *Landscape Connectivity Analysis*

Inverse point density maps of final frog locations after four days allow us to visualize frog dispersal patterns (Figures 3.5 and 3.6). Using these maps as cost surfaces to generate cost connectivity maps among wetlands allows us to visualize priority areas for gopher frog dispersal.

The cost connectivity tool generates a 'PATHCOST' value for each path which represents the total accumulative cost for the path. The range of total least cost paths is 0.42 – 1.23 with an average of 0.53. The average cost per path for each scenario has a range of 0.08 – 0.24 with an average of 0.10. Scenario 10 had the highest average cost per path (0.24) and the largest sum of least cost paths (1.23). The full results of the cost connectivity analysis are shown in Table 3.2. The least cost connectivity tool determined least cost paths exist between the following wetland pairs: 30 – 31, 20 – 30, 20 – 34, 3 – 20, 15 – 20, and 30 – 34. Across all scenarios, the least cost path was between wetlands 30 – 31. The path between wetlands 15 – 20 was the highest cost path in eight out of ten scenarios with 20 – 34 having the highest cost for the remaining two.

The order of the wetlands from least to most cost path between pairs shifts between scenarios. For example, in Scenarios 1 – 5, we reintroduced 500 frogs at each wetland except one of them. Out of these five scenarios, scenarios 2 and 3 were more costly overall than 1, 4, and 5. In each scenario, the highest cost path was from wetlands 15 – 20 and the least cost path was wetlands 30 – 31. This is not surprising due to the proximity of wetlands 30 and 31 and the distance between 20 and 15. Scenario 2 was the only scenario that produced a least cost path

between wetlands 30 and 34. Additionally, the third least cost path changed throughout almost all the first five Scenarios. There was less variation in the second and 4<sup>th</sup> least cost paths for Scenarios 1 – 5.

In Scenarios 6 – 8, we also released 500 frogs at all but one wetland, but we changed the edge of the wetland at which frogs were released. Again, we saw variation in the order of least to most cost paths across these scenarios. In Scenario 4, we released at the eastern edge, but in Scenario 6, we switched to the southern edge. The total cost was slightly higher in scenario 6. Evidently, the only path change between the scenarios was that the connectivity path between wetlands 3 – 20 switched between the second and third least cost places. In Scenarios 5, 7 and 8, we left out wetland 34. In Scenario 7, we changed the release edge of wetland 15. This change resulted in a higher total cost than scenario 5. In scenario 8, we changed the release edge of wetland 20. This resulted in a lower total cost than wetland 5 or 7.

## **Discussion**

Gopher frogs depend on complementary habitats to persist in the landscape (Jensen 2008). Therefore, successful management for gopher frogs must consider both breeding wetlands and upland habitat. Reintroduction efforts have attempted to augment or establish populations by placing captive-reared juveniles at potential breeding wetlands (Terrell and Maerz 2016). In instances where management for gopher frogs is supported by captive-rearing and reintroduction of juveniles, predicting juvenile dispersal into the upland habitat can improve success.

Knowledge of dispersal patterns is important because amphibian population persistence depends on juvenile survival and dispersal (Semlitsch 2008). To mitigate these challenges researchers often conduct landscape analysis that considers connectivity of breeding wetlands (Chandler et

al. 2015; Brooks et al. 2019). However, many of these models focus on predicting metapopulation dynamics using occupancy or genetics. While these are both valid approaches, it does little to inform managers of what spaces individuals are using during dispersal. For gopher frogs, models that predict broad-scale metapopulation dynamics and population viability analyses of gopher frogs currently contribute to management efforts (e.g., Crawford et al. 2022a; Crawford et al. 2022b), however they lack the finer scale needed to assess management of localized sites. This can become problematic because pond-breeding amphibians are known to exhibit low-levels of population synchrony, both within and between populations (Cayeula et al. 2020). Therefore, it is important that we use generate site specific predictions to inform management decisions. Thus, we built a model that predicts juvenile gopher frog dispersal on ARWMA by utilizing the power of agent-based modelling to simulate a suite of reintroduction scenarios. Given the goals of reinforcing this population, it is imperative that we make informed decisions regarding gopher frog habitat management and reintroduction. This model provides an example of a more applied approach to predicting landscape connectivity for pond-breeding amphibians. Results from these simulations will help guide management actions on ARWMA by determining specific areas that are most important to maximizing landscape connectivity for gopher frogs.

In the scenarios that we simulated; a few patterns emerged. The path from 15-20 and 20-34 were the two mostly costly paths. We believe this was likely due to the distance between wetlands. Likely also due to proximity, the path from 30 – 31 was the least cost path across all scenarios. Furthermore, in scenarios 1 – 5 where number of frogs released and release edge were held constant, scenarios 2 and 3 were the costliest overall, which left out releases at 15 and 20, respectively. By comparing that to scenarios 1, 3, and 5, where both wetlands 15 and 20 were

included in releases, we notice that it may be possible to reduce overall cost if you include those wetlands. However, the distance between them renders that path very high cost. Additionally, scenarios 5, 7 and 8 all left out wetland 34. All three of those scenarios were among the lowest total cost. Similarly, wetland 34 is far from any other wetland, and 20 – 34 was the highest cost path in a few scenarios. Therefore, given these comparisons, prioritizing restoration at wetlands in high-cost areas may lead to increased connectivity on the landscape.

This modelling exercise has limitations. Our suite of simulations demonstrates that this tool can be effective for estimating connectivity between wetlands on ARWMA, however the generic movement model simulates the number of gopher frogs that make it through 4 nights of movement. Since this is such a short amount of time, we recognize that it is difficult to make assumptions about long-term dispersal of juvenile gopher frogs. One reason for this is because juvenile amphibians are hypothesized to have a secondary dispersal stage. It's thought that this dispersal stage occurs after a period in which individuals have settled on the landscape. This hypothesis is supported in gopher frogs. Adult gopher frogs are known to move over 3 kilometers to travel to breeding sites, but distances of that magnitude have never been documented in shorter term dispersal studies (Roznik and Johnson 2009; Humphries and Sisson 2012; Hunt 2019; Thesing, chapter 2; Maerz et al. unpub. data). This highlights a need for future research in gopher frogs. Despite this gap, our model can still be useful to informing management and reintroduction. By simulating short-term dispersal, we can aim to maximize survival prior to any secondary dispersal stage. Furthermore, our priority maps (Figures 3.7 & 3.8) show core areas for juvenile frog dispersal and upland habitation between our priority wetlands. For juvenile frogs to survive and breed in a landscape of connected wetlands, they must have suitable upland habitat where gopher tortoise burrows are a key component.

Telemetry studies have revealed that juvenile frog survival during dispersal is highly dependent on an individual's ability to settle in a gopher tortoise burrow (Roznik and Johnson 2009; Hunt 2019; Maerz et al. unpub. data). Thus, gopher tortoise burrow abundance around wetlands must be considered in reintroduction plans for gopher frogs.

Another limitation of this exercise is that none of these scenarios have undergone any rigorous statistical testing. The purpose of the exercise was to build a model that can help visualize where reintroduced gopher frogs will disperse on the landscape and show how varying release scenarios can potentially influence overall landscape connectivity. Because of this, we cannot currently make any specific recommendations regarding release scenarios, but we can demonstrate the power of this tool for future use. We will present this tool to managers at GADNR to collaborate on making more informed decisions to support gopher frog conservation efforts. This tool will help us identify areas that may be of priority when considering gopher frog releases, so that we can make specific recommendations to land managers as to managing the upland on Alapaha River Wildlife Management Area.

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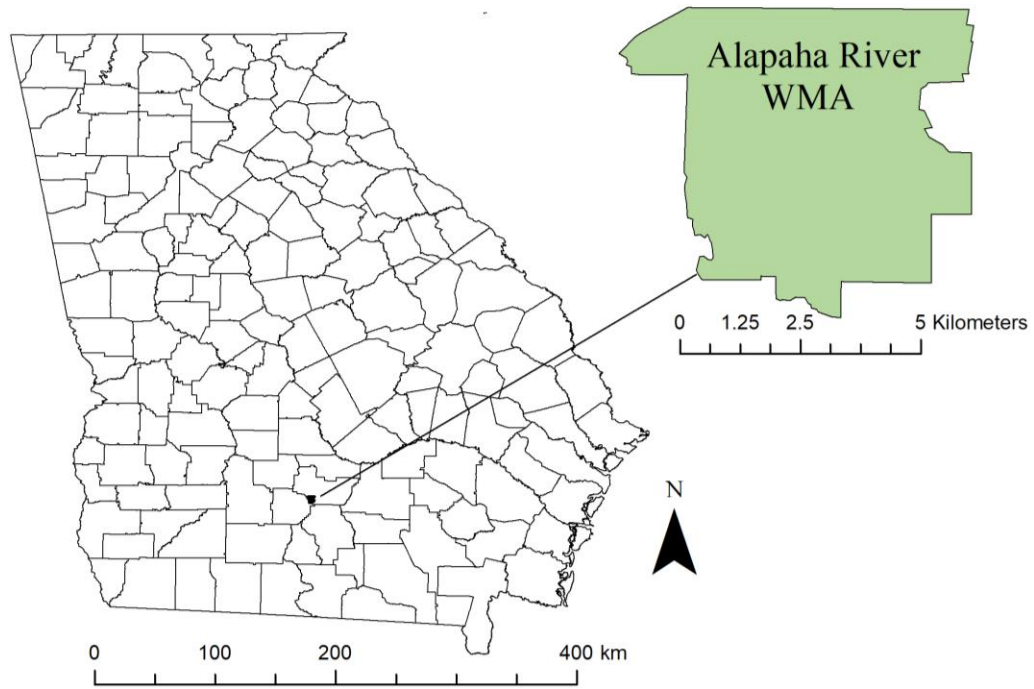


Figure 3.1. A map showing the location of Alapaha River Wildlife Management Area in Irwin county, Georgia, USA. The inset shows the boundary of the property.

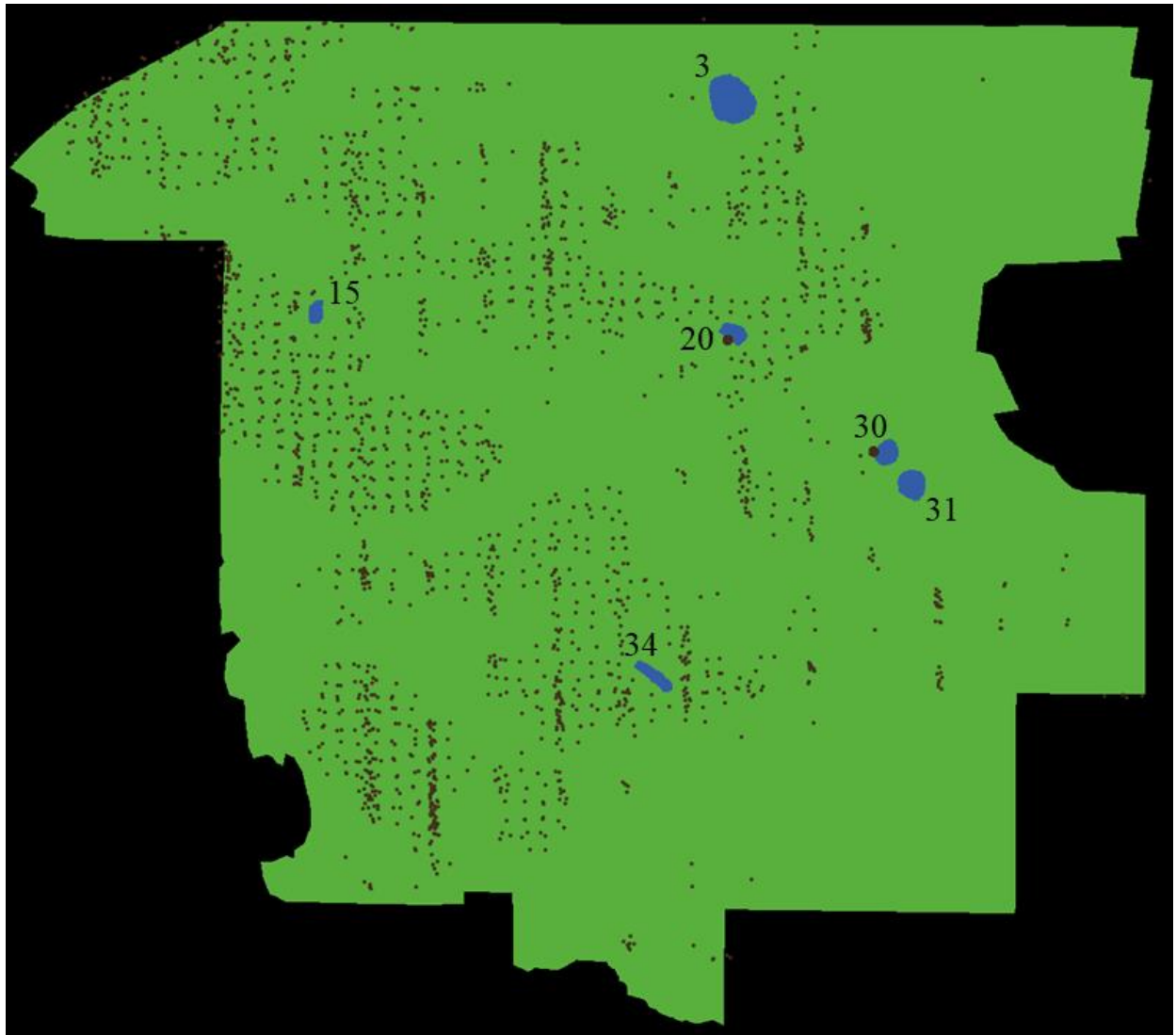


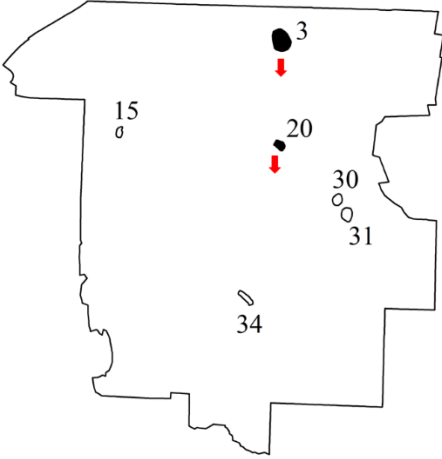
Figure 3.2. The Netlogo landscape showing ARWMA boundary (green), gopher tortoise burrows (dots), and priority wetlands (labeled - blue polygons).

Table 3.1. The ten release scenarios simulated in Netlogo.

<b>Scenario 1</b>	<b>Released? (Yes/No)</b>	<b>Number released</b>	<b>Wetland Edge</b>	<b>Scenario Visualization</b>
Wetland 34	Yes	500	North	
Wetland 30	Yes	500	West	
Wetland 20	Yes	500	South	
Wetland 15	Yes	500	East	
Wetland 3	No	-	-	
<b>Scenario 2</b>				
Wetland 34	Yes	500	North	
Wetland 30	Yes	500	West	
Wetland 20	No	-	-	
Wetland 15	Yes	500	East	
Wetland 3	Yes	500	South	
<b>Scenario 3</b>				
Wetland 34	Yes	500	North	
Wetland 30	Yes	500	West	
Wetland 20	No	500	South	
Wetland 15	Yes	-	-	
Wetland 3	Yes	500	South	

Scenario 4				
Wetland 34	Yes	500	North	
Wetland 30	No	-	-	
Wetland 20	Yes	500	South	
Wetland 15	Yes	500	East	
Wetland 3	Yes	500	South	
Scenario 5				
Wetland 34	No	-	-	
Wetland 30	Yes	500	West	
Wetland 20	Yes	500	South	
Wetland 15	Yes	500	East	
Wetland 3	Yes	500	South	
Scenario 6				
Wetland 34	Yes	500	North	
Wetland 30	No	-	-	
Wetland 20	Yes	500	South	
Wetland 15	Yes	500	South	
Wetland 3	Yes	500	South	

<b>Scenario 7</b>				
Wetland 34	No	-	-	
Wetland 30	Yes	500	West	
Wetland 20	Yes	500	South	
Wetland 15	Yes	500	South	
Wetland 3	Yes	500	South	
<b>Scenario 8</b>				
Wetland 34	No	-	-	
Wetland 30	Yes	500	West	
Wetland 20	Yes	500	North	
Wetland 15	Yes	500	East	
Wetland 3	Yes	500	South	
<b>Scenario 9</b>				
Wetland 34	No	-	-	
Wetland 30	No	-	-	
Wetland 20	Yes	1000	North	
Wetland 15	Yes	1000	East	
Wetland 3	No	-	-	

Scenario 10				
Wetland 34	No	-	-	
Wetland 30	No	-	-	
Wetland 20	Yes	1000	South	
Wetland 15	No	-	-	
Wetland 3	No	1000	South	

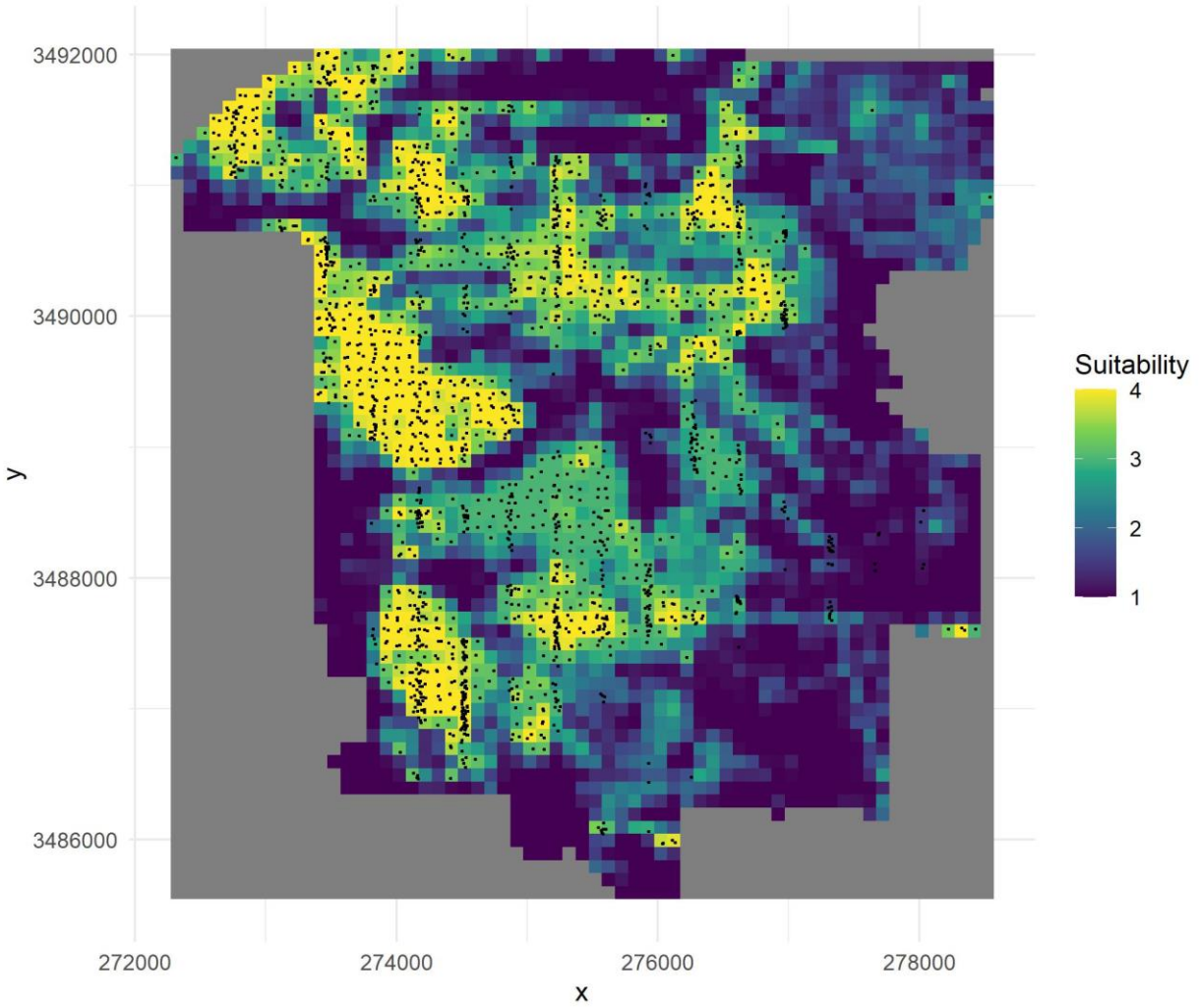


Figure 3.3. A map of ARWMA showing the predicted suitable habitat for gopher tortoises. The warmer colors represent higher suitability. The black dots are predicted locations of gopher tortoise burrows generated by the spatially explicit distance sampling model.

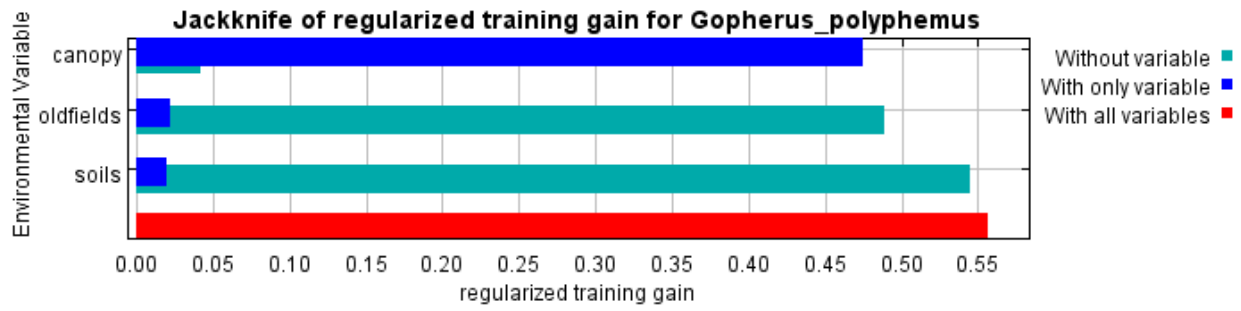


Figure 3.4. Jackknife analysis of variables used to estimate suitable habitat for gopher tortoises on ARWMA.

Table 3.2. The ten release scenarios and the results from the landscape connectivity analysis. Least to most cost path should be read left to right.

<b>Release Scenario</b>	<b>Total Cost</b>	<b>Least to Most Cost Paths</b>					<b>Average Cost per path</b>
<b>1</b>	0.50	0.009 (30 – 31)	0.02 (20 – 30)	0.08 (20 – 34)	0.16 (3 – 20)	0.21 (15 – 20)	0.10
<b>2</b>	0.53	0.007 (30 – 31)	0.08 (20 – 30)	0.09 (30 – 34)	0.11 (3 – 20)	0.23 (15 – 20)	0.10
<b>3</b>	0.53	0.009 (30 – 31)	0.03 (20 – 30)	0.07 (3 – 20)	0.09 (20 – 34)	0.31 (15 – 20)	0.10
<b>4</b>	0.43	0.013 (30 – 31)	0.04 (3 – 20)	0.08 (20 – 30)	0.13 (20 – 34)	0.15 (15 – 20)	0.08
<b>5</b>	0.43	0.007 (30 – 31)	0.01 (20 – 30)	0.05 (3 – 20)	0.17 (20 – 34)	0.18 (15 – 20)	0.08
<b>6</b>	0.46	0.014 (30 – 31)	0.05 (3 – 20)	0.07 (20 – 30)	0.13 (20 – 34)	0.18 (15 – 20)	0.09
<b>7</b>	0.44	0.007 (30 – 31)	0.01 (20 – 30)	0.05 (3 – 20)	0.16 (20 – 34)	0.20 (15 – 20)	0.08
<b>8</b>	0.42	0.007 (30 – 31)	0.01 (20 – 30)	0.03 (3 – 20)	0.18 (15 – 20)	0.18 (20 – 34)	0.08
<b>9</b>	0.40	0.01 (30 – 31)	0.03 (15 – 20)	0.04 (20 – 30)	0.04 (3 – 20)	0.26 (20 – 34)	0.08
<b>10</b>	1.23	0.01 (30 – 31)	0.02 (20 – 30)	.29 (3 – 20)	.32 (20 – 34)	.56 (15 – 20)	0.24

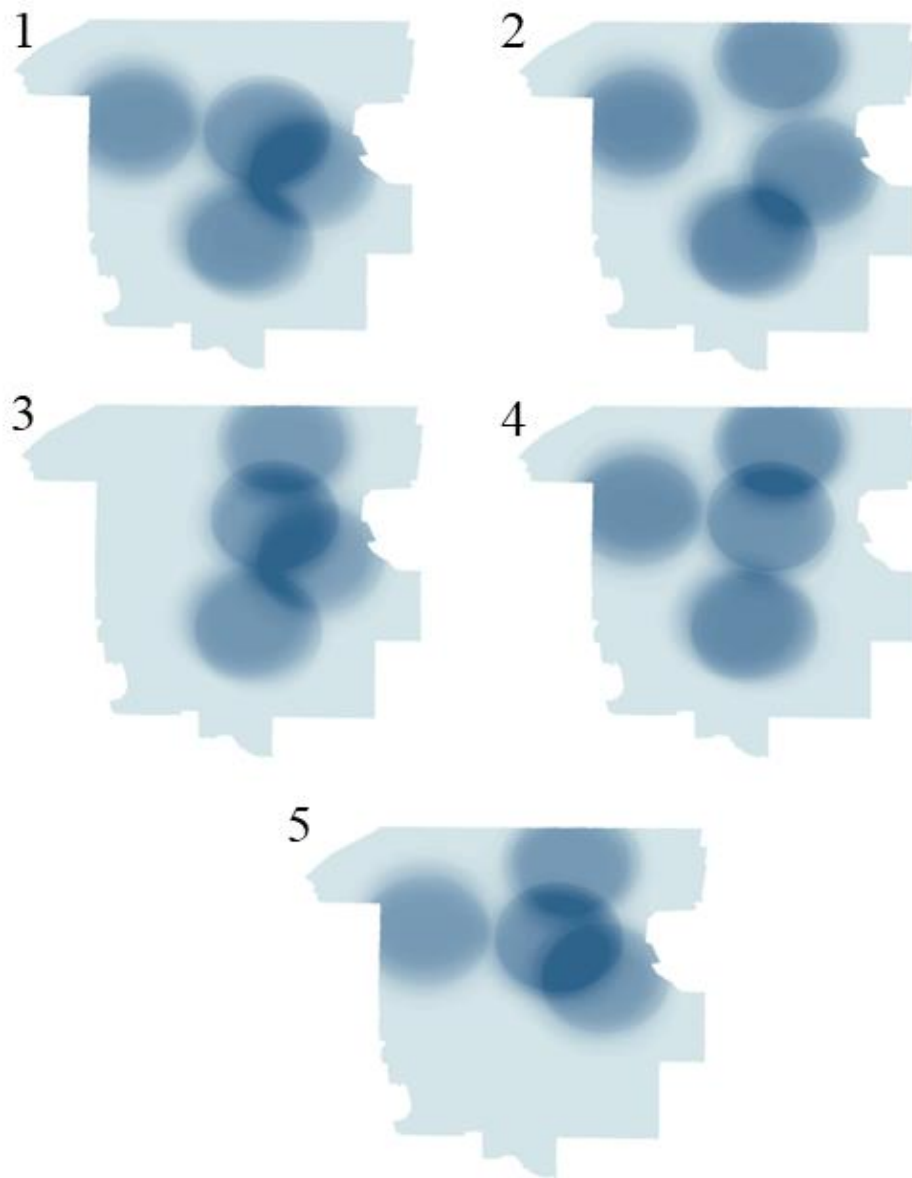


Figure 3.5. Scenarios 1 – 5 showing the inverse point density of frogs between priority wetlands. The darker color indicate a higher density of frogs.

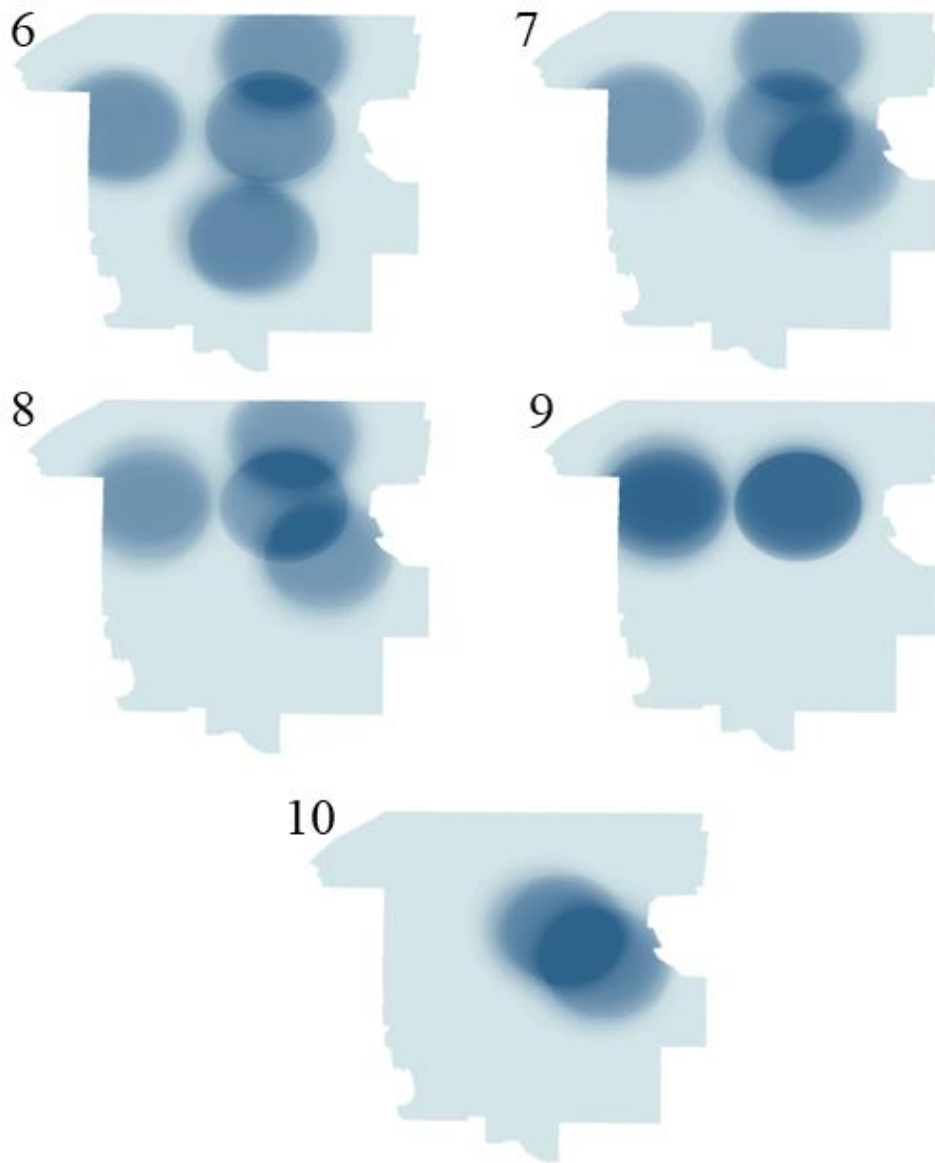


Figure 3.7. Scenarios 6 – 10 showing the inverse point density of frogs between priority wetlands. The darker color indicate a higher density of frogs.

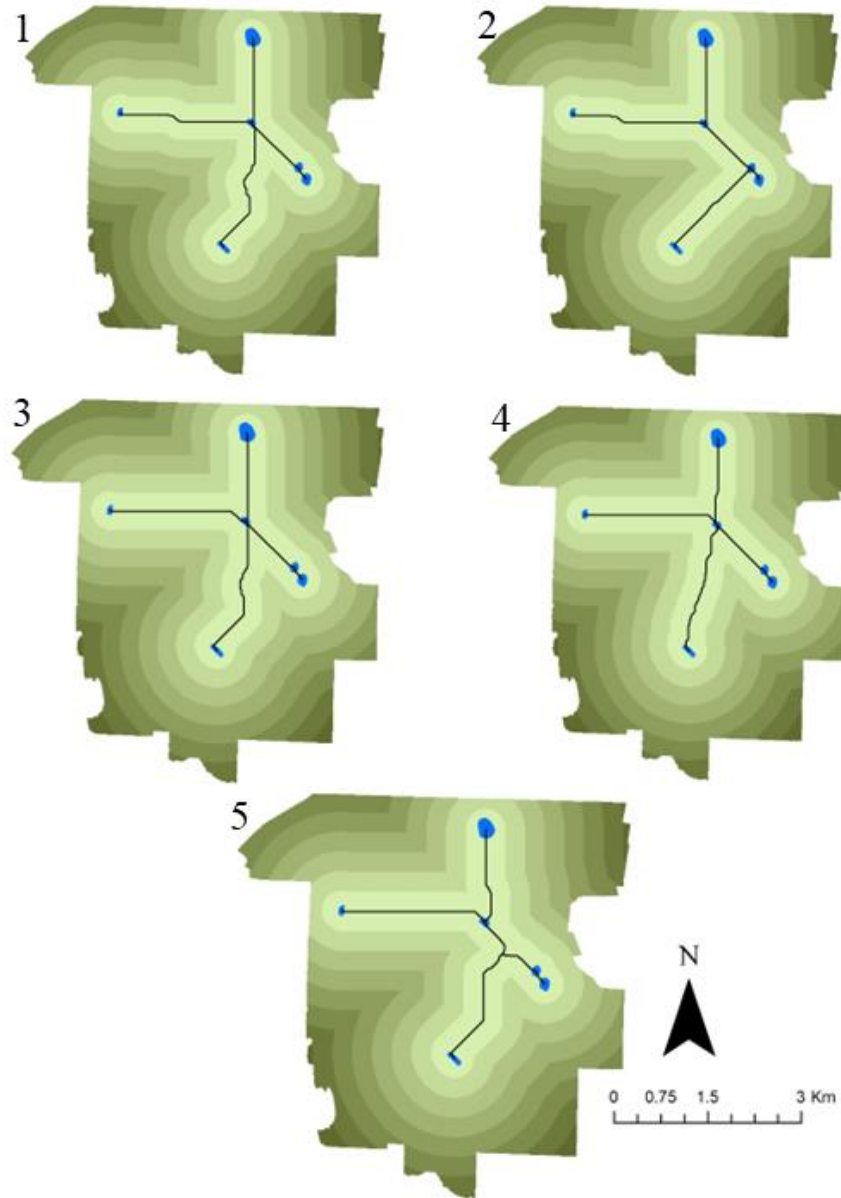


Figure 3.7. Scenarios 1 – 5 showing least cost paths of connectivity between priority wetlands. The lighter color indicates an area of higher priority for juvenile gopher frog movement.

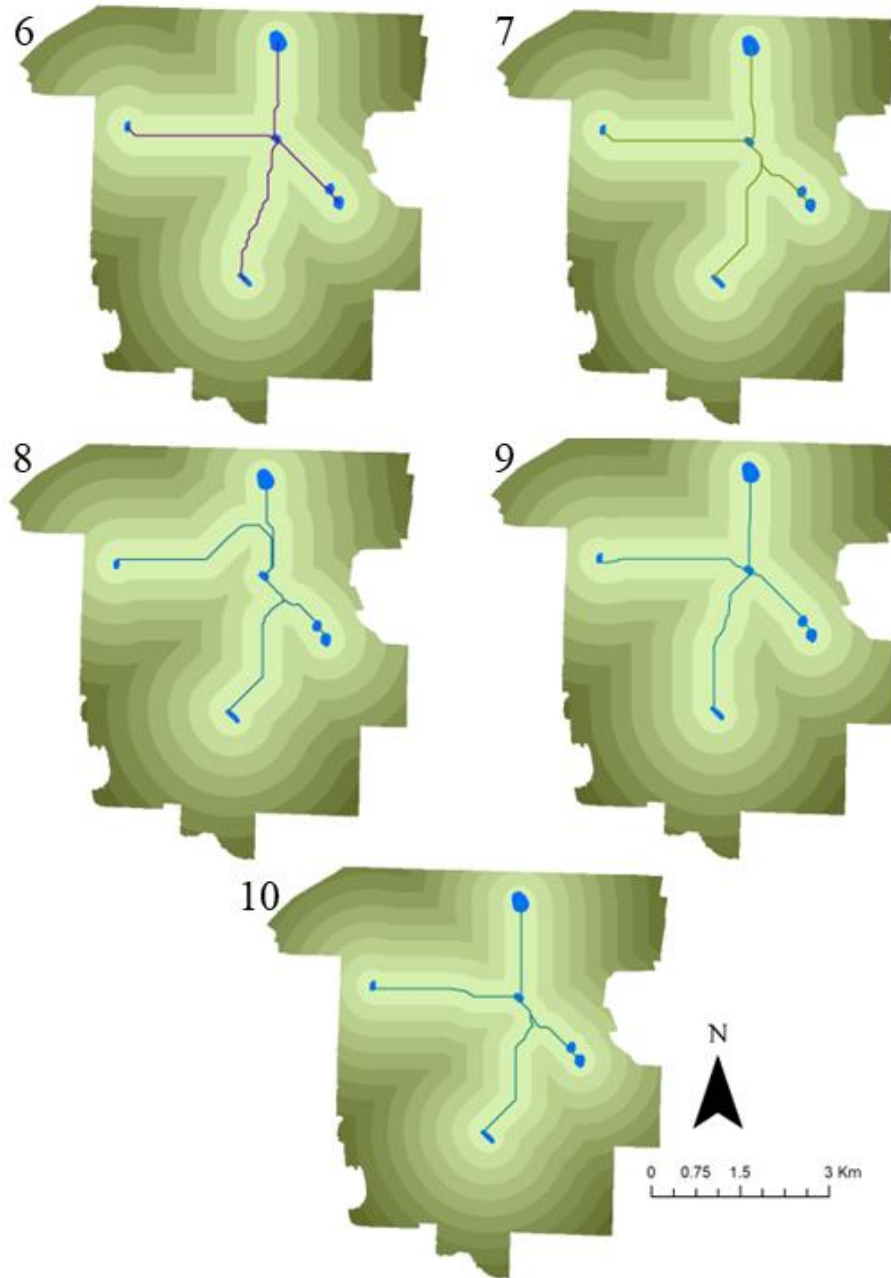


Figure 3.8. Scenarios 6 – 10 showing least cost paths of connectivity between priority wetlands. The lighter color indicates an area of higher priority for juvenile gopher frog movement.

## CHAPTER 4

### CONCLUSIONS

#### *Parameterizing an agent-based model to simulate juvenile Gopher Frog dispersal*

The objective of Chapter 2 was to use data from radiotelemetry to parameterize an agent-based model that accurately simulates juvenile gopher frog dispersal from a single release point. In Chapter 2, we built this model and fit the model to observed patterns of juvenile gopher frog movement. Given that we successfully fit our model to observed net displacement distances by comparing the distributions of simulated net displacements vs. observed net displacements, we can make a reasonable assumption that the model is realistic. The frog-radius parameter also attempts to explain the role of burrow detection in dispersal. The 1m frog-radius was the only value that fit to our observed data, however, there is still a visual gap between empirical cumulative distribution function (ECDF) curves. We believe this occurs because of two reasons. First, the observed distributions are formed from far less data than those from model simulations. This accounts for the jaggedness of the observed curve. Secondly, the movement parameters (turning angle and step-length) come from telemetry data conducted on landscapes where burrows were not randomly placed, like in our model. Additionally, Gopher frog distribution on the landscape aligns with distribution of gopher tortoise burrows (Marshall et al. 2023). Therefore, the gaps in distance between 1m frog radius and observed data in ECDF function may demonstrate that burrow placement bias. Because there is evidence to suggest that finding a

burrow boosts the survival probability of an individual, understanding the ability to find a burrow and role of the number of burrows is important to determining success of reintroduced individuals on the landscape.

Understanding the sensitivity of the model parameters is critical to making inferences about the model results. It's not surprising that net displacement was most sensitive to step-length, because both are distance metrics. However, net displacement was almost just as sensitive to probability of movement. This likely means that this parameter is successful at capturing some of the movement variation due to habitat, weather, or other conditions affecting movement that are not explicitly defined in the model. While not as sensitive, daily survival and probability of stopping also likely capture behavioral variation caused by external factors. Net displacement was not quite as sensitive to the number of burrows, the degree of sensitivity it does show supports the idea that gopher tortoise burrows are an essential resource to juvenile gopher frogs. The last movement parameter, turning angle, showed some sensitivity to a higher turning angle, but no sensitivity to lower turning angles. We don't often observe juvenile gopher frogs making drastic changes in direction relative to their distance traveled, so turn angle likely has little effect on net displacement. However, this model does not assess turning angles should an individual encounter unsuitable habitat.

The advantage to incorporating parameters that account for variation that might be difficult to measure is that it allows us to apply the model to different scenarios where flexibility is crucial. For example, future reintroductions of gopher frogs may take place at different wetlands on the same properties or different properties altogether. Because we don't include site specific attributes yet include parameters in the model that allow for variation and flexibility, we can apply this ABM to future reintroduction sites to observe patterns of juvenile gopher frog

dispersal before reintroduction takes place. Doing so will allow us to make more informed decisions on whether to release at a certain site, the exact release points, and how many individuals to release.

### *Applying juvenile Gopher Frog dispersal model on Alapaha River Wildlife Management Area*

Chapter 3 focused on applying the movement model to simulating different gopher frog reintroduction scenarios at Alapaha River Wildlife Management Area (ARWMA) in Georgia, USA. Our objective in Chapter 3 was to compare the landscape connectivity for juvenile gopher frogs under different release scenarios. We built an ABM to simulate different reintroduction scenarios where we varied which wetlands we release at, number of frogs released, and wetland edge. By doing so and completing these objectives, we demonstrated that this tool can be used to inform Gopher Frog reintroduction and management on ARWMA.

In the scenarios that we simulated; a few patterns emerged. The path from 15-20 and 20-34 were the two mostly costly paths. We believe this was likely due to the distance between wetlands. Likely also due to proximity, the path from 30 – 31 was the least cost path across all scenarios. Furthermore, in scenarios 1 – 5 where number of frogs released and release edge were held constant, scenarios 2 and 3 were the costliest overall, which left out releases at 15 and 20, respectively. By comparing that to scenarios 1, 3, and 5, where both wetlands 15 and 20 were included in releases, we notice that it may be possible to reduce overall cost if you include those wetlands. However, the distance between them renders that path very high cost. Additionally, scenarios 5, 7 and 8 all left out wetland 34. All three of those scenarios were among the lowest total cost. Similarly, wetland 34 is far from any other wetland, and 20 – 34 was the highest cost

path in a few scenarios. Therefore, given these comparisons, prioritizing restoration at wetlands in high-cost areas may lead to increased connectivity on the landscape.

This modelling exercise has limitations. Our suite of simulations demonstrates that this tool can be effective for estimating connectivity between wetlands on ARWMA, however the generic movement model simulates the number of gopher frogs that make it through 4 nights of movement. Since this is such a short amount of time, we recognize that it is difficult to make assumptions about long-term dispersal of juvenile gopher frogs. One reason for this is because juvenile amphibians are hypothesized to have a secondary dispersal stage. It's thought that this dispersal stage occurs after a period in which individuals are thought to have settled on the landscape. This hypothesis is supported in gopher frogs. Adult gopher frogs are known to move over 3 kilometers to travel to breeding sites (Humphries and Sisson 2012), but distances of that magnitude have never been documented in shorter term dispersal studies (Roznik and Johnson 2009; Hunt 2019; Thesing, Chapter 2; Maerz et al. unpub. data). This highlights a need for future research in gopher frogs. Despite this gap, our model can still be useful to informing management and reintroduction. By simulating short-term dispersal, we can aim to maximize survival prior to any secondary dispersal stage. Furthermore, our priority maps show core areas for juvenile frog dispersal and upland habitation between our priority wetlands. For juvenile frogs to survive and breed in a landscape of connected wetlands, they must have suitable upland habitat where gopher tortoise burrows are a key component. Telemetry studies have revealed that juvenile frog survival during dispersal is highly dependent on an individual's ability to settle in a gopher tortoise burrow (Roznik and Johnson 2009; Hunt 2019; Maerz et al. unpub. data). Thus, gopher tortoise burrow abundance around wetlands must be considered in reintroduction plans for gopher frogs.

Another limitation of this exercise is that none of these scenarios have undergone any rigorous statistical testing. The purpose of the exercise was to build a model that can help visualize where reintroduced gopher frogs will disperse on the landscape and show how varying release scenarios can potentially influence overall landscape connectivity. Because of this, we cannot currently make any specific recommendations regarding release scenarios, but we can demonstrate the power of this tool for future use. We will present this tool to managers at GADNR to collaborate on making more informed decisions to support gopher frog conservation efforts. This tool will help us identify areas that may be of priority when considering gopher frog releases, so that we can make specific recommendations to land managers as to managing the upland on Alapaha River Wildlife Management Area.

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## Appendix 2.1: Netlogo code for simulating generic juvenile gopher frog dispersal

```
;;global variables
;; patch variables (characteristics)
;; turtle variables (survival, etc) but with frogs

extensions [ csv nw ]
globals [ frog-count frog-list frog-dist frog-d1 ref-list av-net-dist ]
breed [frogs frog]
breed [ refugias refugia ]

refugias-own [ ref-type ]
frogs-own [

  net-dist
  actual-d1-dist
  actual-d2-dist
  actual-d3-dist
  actual-d4-dist
  day1-dist
  day2-dist
  day3-dist
  day4-dist
  moved-n2?
  moved-n3?
  moved-n4?
  day1-none-ref
  day2-none-ref
  day3-none-ref
  day4-none-ref
  day1-temp-found
  day2-temp-found
  day3-temp-found
  day4-temp-found
  day1-perm-found
  day2-perm-found
  day3-perm-found
  day4-perm-found
  left?
  moving?
  n1-attempt
  n2-attempt
  n3-attempt
  n4-attempt
  n1
  n2
  n3
  n4
  moving?

]

to set-up
```

```

;;clears the last setup
ca

ask patches

[set pcolor 56]

create-refugia

;; gopher frog shape

reintroduce-frogs
set frog-list []
set frog-dl []
set frog-count count turtles

reset-ticks

end

to create-refugia

; let refugia-std-dev burrow-clustering - num-burrow-clusters
; let burrow-cluster-size num-burrows / num-burrow-clusters
; repeat num-burrow-clusters [
;   let center-x random-float 1199
;   let center-y random-float 1199
;   create-refugias burrow-cluster-size [
;     setxy center-x center-y
;     set size 10
;     set color 32
;     set shape "dot"
;     set heading random 360
;     fd abs random-normal 0 (refugia-std-dev / 2) ;; Divide by two because
abs doubles the width
;   ]
; ]

let permanent-refuge (num-burrows)
;let temporary-refuge (2000)

create-refugias permanent-refuge
[
  set shape "dot"
  set xcor random-float 1299
  set ycor random-float 1299
  set size 10
  set color 32
  set ref-type 2

```

```

]

; create-refugias temporary-refuge
; [
;     set shape "plant"
;     set xcor random-float 1199
;     set ycor random-float 1199
;     set size 10
;     set color 52
;     set ref-type 1

; ]

end

to reintroduce-frogs

    create-frogs 50
    [ ask frogs [set shape "frog top"]
      setxy 649 649
      set size 10
      set color brown
      set day1-dist (random-gamma ((dlmean ^ 2) / 5965.15 ) (1 / ( 5965.15 /
dlmean ) ) )
      set day2-dist (random-gamma ((d2mean ^ 2) / 4432.44 ) (1 / ( 4432.44 /
dlmean ) ) )
      set day3-dist (random-gamma ((d3mean ^ 2) / 3025 ) (1 / ( 3025 / dlmean )
))
      set day4-dist (random-gamma ((d4mean ^ 2) / 2472.86 ) (1 / ( 2472.86 /
dlmean ) ) )
      set actual-d1-dist 0
      set actual-d2-dist 0
      set actual-d3-dist 0
      set actual-d4-dist 0
      set moved-n2? 0
      set moved-n3? 0
      set moved-n4? 0
      set left? 0
    set day1-none-ref 0
    set day2-none-ref 0
    set day3-none-ref 0
    set day4-none-ref 0
; set day1-temp-found 0
; set day2-temp-found 0
; set day3-temp-found 0
; set day4-temp-found 0
    set day1-perm-found 0
    set day2-perm-found 0
    set day3-perm-found 0
    set day4-perm-found 0
    set n1-attempt 0
    set n2-attempt 0
    set n3-attempt 0
    set n4-attempt 0
    set n1 0

```

```

set n2 0
set n3 0

]

end

to go
move

if all? frogs [moving? = 0] [stop]

; write-distances-to-csv

end

to move

ask frogs [ pen-down

if n1 = 0 [

if actual-d1-dist >= day1-dist [set day1-none-ref 1 set n1 1 set moving? 0
stop ]

let refuge one-of refugias in-radius frog-radius

if actual-d1-dist = 0 [survive rt random 360 fd 1 set moving? 1 set
actual-d1-dist actual-d1-dist + 1 ]
if actual-d1-dist > 0 [ ifelse refuge != nobody

[ ifelse random-float 1.0 < probability-of-stopping [set day1-perm-found
1 set n1 0 set moving? 0 stop ] [fd 1 set moving? 1 set actual-d1-dist
actual-d1-dist + 1]]

[fd 1 set moving? 1 set actual-d1-dist actual-d1-dist + 1 ] ]

]

if n1 = 1 [

let refuge one-of refugias in-radius frog-radius

ifelse actual-d2-dist >= day2-dist [ set day2-none-ref 1 set n1 3 set n2 1

```

```

set moving? 0 stop]
[
    if day1-none-ref = 1 [survive ifelse random-float 1.0 < probability-of-
movement [rt random-normal d2TAmean 62.0 fd 1 set moving? 1 set day1-none-ref
0 set actual-d2-dist actual-d2-dist + 1 ] [set day1-none-ref 0 set moving? 0
set n1 3 set n2 1 stop]]
    ; if day1-perm-found = 1 [surviveb ifelse random-float 1.0 <
probability-of-movement [rt random-normal d2TAmean 62.0 fd 1 set moving? 1
set day1-perm-found 0 set actual-d2-dist actual-d2-dist + 1 ] [set day1-perm-
found 0 set moving? 0 set n1 3 set n2 1 stop]]

    if actual-d2-dist > 0 [ ifelse refuge != nobody

        [ ifelse random-float 1.0 < probability-of-stopping [set day2-perm-
found 1 set moving? 0 set n1 3 set n2 1 stop ] [fd 1 set moving? 1 set actual-
d2-dist actual-d2-dist + 1]]

        [fd 1 set moving? 1 set actual-d2-dist actual-d2-dist + 1] ]
    ]

]

if n2 = 1 [
    let refuge one-of refugias in-radius frog-radius

    ifelse actual-d3-dist >= day3-dist [ set day3-none-ref 1 set n2 0 set n3 1
set moving? 0 stop ]
    [
        if day2-none-ref = 1 [ survive ifelse random-float 1.0 < probability-
of-movement [rt random-normal d3TAmean59.3 fd 1 set moving? 1 set day2-none-
ref 0 set actual-d3-dist actual-d3-dist + 1 ] [ set day2-none-ref 0 set n2 0
set n3 1 set moving? 0 stop]]

        ; if day2-perm-found = 1 [surviveb ifelse random-float 1.0 <
probability-of-movement [rt random-normal d3TAmean 59.3 fd 1 set moving? 1
set day2-perm-found 0 set actual-d3-dist actual-d3-dist + 1 ] [ set day2-
perm-found 0 set n2 0 set n3 1 set moving? 0 stop]]

        if actual-d3-dist > 0 [ ifelse refuge != nobody

            [ ifelse random-float 1.0 < probability-of-stopping [set day3-perm-
found 1 set n2 0 set n3 1 set moving? 0 stop ] [fd 1 set moving? 1 set
actual-d3-dist actual-d3-dist + 1]]

            [fd 1 set moving? 1 set actual-d3-dist actual-d3-dist + 1] ]
        ]
    ]
]

```

```

]

if n3 = 1 [

  let refuge one-of refugias in-radius frog-radius

  ifelse actual-d4-dist >= day4-dist [ set day4-none-ref 1 set n3 2 set
moving? 0 set net-dist distancexy 649 649 stop ] [

    if day3-none-ref = 1 [survive ifelse random-float 1.0 < probability-of-
movement [rt random-normal d4TAMean 79.3 fd 1 set moving? 1 set day3-none-ref
0 set actual-d4-dist actual-d4-dist + 1 ] [set day3-none-ref 0 set n3 2 set
moving? 0 set net-dist distancexy 649 649 stop]]

    ;if day3-perm-found = 1 [surviveb ifelse random-float 1.0 <
probability-of-movement [rt random-normal d4TAMean 79.3 fd 1 set moving? 1
set day3-perm-found 0 set actual-d4-dist actual-d4-dist + 1 ] [ set day3-perm-
found 0 set n3 2 set moving? 0 set net-dist distancexy 649 649 stop]]

    if actual-d4-dist > 0 [ ifelse refuge != nobody

      [ ifelse random-float 1.0 < probability-of-stopping [set day4-perm-
found 1 set n3 2 set moving? 0 set net-dist distancexy 649 649 stop ] [fd 1
set moving? 1 set actual-d4-dist actual-d4-dist + 1]]

      [fd 1 set moving? 1 set actual-d4-dist actual-d4-dist + 1] ]

    ]

  ]

end

to survive

  if random-float 1.0 > survival-probability [die]

end

to surviveb

  ;; if random-float 1.0 > survival-burrow [die]

end

to write-distances-to-csv

  csv:to-file "prelim_netdist_move_ps1_test3.csv" [ (list distancexy 599 599)
] of frogs

end

```

```
to-report net-displacements-csv

  let net-dists [ (list who distancexy 649 649) ] of frogs
  report csv:to-string fput ["who" "net-dist"] net-dists

; report csv:to-string
; fput ["net-dists"]
; [(list distancexy 649 649)] of frogs

end
```

## Appendix 3.1: Netlogo code for simulating juvenile gopher frog reintroduction scenarios on Alapaha River Wildlife Management Area

```
extensions [ gis ]

globals [ landscape gtburrows release-points ]

patches-own [ land-value ]

breed [ burrows burrow ]

breed [ frogs frog ]

frogs-own [ net-dist
  actual-d1-dist
  actual-d2-dist
  actual-d3-dist
  actual-d4-dist
  day1-dist
  day2-dist
  day3-dist
  day4-dist
  day1-none-ref
  day2-none-ref
  day3-none-ref
  day4-none-ref
  day1-perm-found
  day2-perm-found
  day3-perm-found
  day4-perm-found
  left?
  moving?
  n1
  n2
  n3
]

burrows-own [ ]

to set-up

  clear-all

  gis:load-coordinate-system ("landscape.prj")

  set landscape gis:load-dataset "landscape.asc"
  set gtburrows gis:load-dataset "burrows_final.shp"
  set release-points gis:load-dataset "Release_10.shp"

  let width floor (gis:width-of landscape / 4)
```

```

let height floor (gis:height-of landscape / 4)
resize-world (-1 * width ) width (-1 * height ) height

set-patch-size 1

gis:set-world-envelope-ds gis:envelope-of landscape

gis:apply-raster landscape land-value

ask patches [

  ;set land-value gis:raster-sample landscape self

  if land-value = 1 [ set pcolor green ]
  if land-value > 1 [ set pcolor blue ]

]

foreach gis:feature-list-of gtburrows [
  vector-feature ->
  let coords gis:location-of (first (first (gis:vertex-lists-of vector-
feature)))

  let long-coord item 0 coords
  let lat-coord item 1 coords

  create-burrows 1 [ setxy long-coord lat-coord set shape "dot" set color
32 set size 10]
]

foreach gis:feature-list-of release-points [
  vector-feature ->
  let release-coords gis:location-of (first (first (gis:vertex-lists-of
vector-feature)))

  let release-long-coord item 0 release-coords
  let release-lat-coord item 1 release-coords

  create-frogs 1000 [ setxy release-long-coord release-lat-coord
  set shape "frog top"
  set color 32
  set size 10
  set day1-dist (random-gamma 1.893 0.0178) / 4
  set day2-dist (random-gamma 1.617 0.0191 ) / 4
  set day3-dist (random-gamma 1.21 0.02 ) / 4
  set day4-dist (random-gamma 1.308 0.023) / 4
  set actual-d1-dist 0
  set actual-d2-dist 0
  set actual-d3-dist 0
  set actual-d4-dist 0
  set day1-none-ref 0
  set day2-none-ref 0
  set day3-none-ref 0

```

```

    set day4-none-ref 0
    set day1-perm-found 0
    set day2-perm-found 0
    set day3-perm-found 0
    set day4-perm-found 0
    set n1 0
    set n2 0
    set n3 0
  ]
]

end

to release-frogs

  ask frogs [ pen-down

  if n1 = 0 [
    avoid-wetland

    if actual-d1-dist >= day1-dist [set day1-none-ref 1 set n1 1 set moving? 0
stop ]

    let refuge one-of burrows in-radius 1

    if actual-d1-dist = 0 [survive rt random 360 fd 1 set moving? 1 set
actual-d1-dist actual-d1-dist + 1 ]
    if actual-d1-dist > 0 [ ifelse refuge != nobody

      [ ifelse random-float 1.0 < probability-of-stopping [set day1-perm-found
1 set n1 0 set moving? 0 stop ] [fd 1 set moving? 1 set actual-d1-dist
actual-d1-dist + 1]]

      [fd 1 set moving? 1 set actual-d1-dist actual-d1-dist + 1 ] ]

  ]

  if n1 = 1 [

    let refuge one-of burrows in-radius 1

    ifelse actual-d2-dist >= day2-dist [ set day2-none-ref 1 set n1 3 set n2 1
set moving? 0 stop]
    [

```

```

avoid-wetland

    if day1-none-ref = 1 [survive ifelse random-float 1.0 < probability-of-
movement [rt random-normal 3.38 62.0 fd 1 set moving? 1 set day1-none-ref 0
set actual-d2-dist actual-d2-dist + 1 ] [set day1-none-ref 0 set moving? 0
set n1 3 set n2 1 stop]]
    ; if day1-perm-found = 1 [surviveb ifelse random-float 1.0 <
probability-of-movement [rt random-normal d2TAMean 62.0 fd 1 set moving? 1
set day1-perm-found 0 set actual-d2-dist actual-d2-dist + 1 ] [set day1-perm-
found 0 set moving? 0 set n1 3 set n2 1 stop]]

    if actual-d2-dist > 0 [ ifelse refuge != nobody

        [ ifelse random-float 1.0 < probability-of-stopping [set day2-perm-
found 1 set moving? 0 set n1 3 set n2 1 stop ] [fd 1 set moving? 1 set actual-
d2-dist actual-d2-dist + 1]]

        [fd 1 set moving? 1 set actual-d2-dist actual-d2-dist + 1] ]

    ]

]

if n2 = 1 [

    let refuge one-of burrows in-radius 1

    ifelse actual-d3-dist >= day3-dist [ set day3-none-ref 1 set n2 0 set n3 1
set moving? 0 stop ]
    [
        avoid-wetland

        if day2-none-ref = 1 [ survive ifelse random-float 1.0 < probability-
of-movement [rt random-normal -41.8 59.3 fd 1 set moving? 1 set day2-none-
ref 0 set actual-d3-dist actual-d3-dist + 1 ] [ set day2-none-ref 0 set n2 0
set n3 1 set moving? 0 stop]]

        ; if day2-perm-found = 1 [surviveb ifelse random-float 1.0 <
probability-of-movement [rt random-normal d3TAMean 59.3 fd 1 set moving? 1
set day2-perm-found 0 set actual-d3-dist actual-d3-dist + 1 ] [ set day2-
perm-found 0 set n2 0 set n3 1 set moving? 0 stop]]

        if actual-d3-dist > 0 [ ifelse refuge != nobody

            [ ifelse random-float 1.0 < probability-of-stopping [set day3-perm-
found 1 set n2 0 set n3 1 set moving? 0 stop ] [fd 1 set moving? 1 set
actual-d3-dist actual-d3-dist + 1]]

            [fd 1 set moving? 1 set actual-d3-dist actual-d3-dist + 1] ]

        ]

    ]

]

```

```

if n3 = 1 [
  let refuge one-of burrows in-radius 1

  ifelse actual-d4-dist >= day4-dist [ set day4-none-ref 1 set n3 2 set
moving? 0 set net-dist distancexy 649 649 stop ][

  avoid-wetland

  if day3-none-ref = 1 [survive ifelse random-float 1.0 < probability-of-
movement [rt random-normal -0.481 79.3 fd 1 set moving? 1 set day3-none-ref 0
set actual-d4-dist actual-d4-dist + 1 ][set day3-none-ref 0 set n3 2 set
moving? 0 set net-dist distancexy 649 649 stop]]

  ;if day3-perm-found = 1 [surviveb ifelse random-float 1.0 <
probability-of-movement [rt random-normal d4TAMean 79.3 fd 1 set moving? 1
set day3-perm-found 0 set actual-d4-dist actual-d4-dist + 1 ][ set day3-perm-
found 0 set n3 2 set moving? 0 set net-dist distancexy 649 649 stop]]

  if actual-d4-dist > 0 [ ifelse refuge != nobody

    [ ifelse random-float 1.0 < probability-of-stopping [set day4-perm-
found 1 set n3 2 set moving? 0 set net-dist distancexy 649 649 stop ] [fd 1
set moving? 1 set actual-d4-dist actual-d4-dist + 1]]

    [fd 1 set moving? 1 set actual-d4-dist actual-d4-dist + 1] ]

  ]
]
]

end

to avoid-wetland

  if [pcolor] of patch-ahead 1 = blue [ set heading heading - 180 ]

end

to survive

  if random-float 1.0 > survival-probability [die]

end

to export-frog-locations-to-csv

  file-open "frog-points_10.csv" ask frogs

  [

    file-type item 1 gis:envelope-of frog who

```

```
file-type ","  
file-type item 3 gis:envelope-of frog who  
file-type "\n"  
  
]  
  
file-close  
  
end
```