GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*) ECOLOGY WITHIN A PRIVATE, WORKING FOREST LANDSCAPE

by

CRAIG DANIEL MARSHALL

(Under the Direction of John C. Maerz and James A. Martin)

ABSTRACT

Uncertainty exists regarding the status of gopher tortoise (*Gopherus polyphemus*) populations range wide. This uncertainty and the recent proposal by the United States Fish and Wildlife Service to reevaluate the species' designation (i.e., threatened) has stimulated research aimed at identifying tortoise population demographics and viability, movement patterns, and habitat associations throughout the species' range. Private, working forest landscapes are ubiquitous across the tortoises' range and populations are known to inhabit and persist within these forests, warranting their integration into tortoise conservation strategies. However, this can be difficult, as there is an incomplete understanding of how tortoises interact with these landscapes. Therefore, the objectives of this study were to estimate abandoned and active tortoise burrow density, evaluate adult tortoise use, and identify vertebrate burrow commensals within a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA. Results from my study indicate that permanently open areas, such as forest roads and utility rights-of-way, and forest stands characterized by early successional vegetation conditions may interact to support tortoise populations within these landscapes. My results also indicate that the adoption of spatially explicit distance sampling models can improve our understanding of the factors influencing tortoise density, such as distance to roads, that are difficult to quantify using standard distance sampling methods. Furthermore, I documented similar use of abandoned, active, and inactive tortoise burrows by vertebrate commensals, indicating the importance of maintaining these structures on the landscape regardless of classification.

INDEX WORDS: Gopher tortoise, *Gopherus polyphemus*, resource selection, distance sampling, spatially explicit, density, private working forests, *Pinus taeda*, loblolly pine, burrow commensals

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DEDICATION

To John “Fogg” Foggia.

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CHAPTER 1

INTRODUCTION & LITERATURE REVIEW

The gopher tortoise (*Gopherus polyphemus*; hereafter, tortoise) is an ecologically important species endemic to the Coastal Plain ecoregion of the southeastern United States (e.g., Young and Goff 1939, Lips 1991, Kinlaw and Grasmueck 2012, Dziadzio and Smith 2016, Potash et al. 2020). Within the last 100 years, tortoise populations have experienced precipitous declines that have been attributed to habitat loss (e.g., conversion to agriculture and forestry), fragmentation, and degradation (e.g., suppression of natural disturbance regimes), disease, and human exploitation (e.g., Hermann et al. 2002, McCoy et al. 2006, Berish and Leone 2014). In response to these long-term declines, tortoise populations west of the Mobile and Tombigbee Rivers in Alabama, Mississippi, and Louisiana, USA were listed as threatened under the federal Endangered Species Act (U.S. Fish and Wildlife Service 1987). Tortoise populations east of these river systems in Alabama, Florida, Georgia, and South Carolina, USA were designated as a candidate species (U.S. Fish and Wildlife Service 2011). Current uncertainty regarding the status of tortoise populations and a recent proposal to reevaluate the species' designation (i.e., threatened) by the United States Fish and Wildlife Service has prompted research aimed at identifying tortoise population demographics and viability, movement patterns, and habitat associations throughout its range (e.g., Greene et al. 2019, Duffie 2020, Greene et al. 2020, Folt et al. 2021).

Private lands have received considerable attention with regards to their capacity to support tortoise populations and aid in conservation strategies (Hermann et al. 2002, Underwood et al. 2012). Currently, private lands encompass > 80% of the species' range; however, these landscapes, especially private working lands, remain relatively understudied with regards to tortoise ecology (Hermann et al. 2002, Underwood et al. 2012, Greene et al. 2020). Private, working forest landscapes are common within the range of the tortoise and tortoises are known to inhabit and persist within these landscapes (Jones and Dorr 2004, Wigley et al. 2012, Duffie 2020). This warrants the integration of these landscapes into conservation strategies; however, limited information exists regarding tortoise ecology within these landscapes, especially under more contemporary forest management practices (Greene et al. 2020, Duffie 2020). Therefore, identifying tortoise demographics, use, and habitat associations within private, working forests, particularly under contemporary management practices, is important to understanding the compatibility of these forests with tortoise conservation.

Commensurate with improving our understanding of tortoise ecology within private, working landscapes is the need to adopt spatially explicit distance sampling models to estimate tortoise density. Conventional distance sampling methods rely on plot-level effects (e.g., vegetation structure and composition) to explain spatial variation in tortoise density (Nomani et al. 2008, Smith et al. 2009, Stober and Smith 2010, Castellon et al. 2015, Gaya 2019, Duffie 2020). Given that sampling grain has been shown to influence relationships between tortoises and vegetation conditions (e.g., canopy cover, groundcover), it may be advantageous to adopt spatially explicit models that can capture variations in tortoise density within sampled plots (Catano et al. 2014, Mizel et al. 2018). Furthermore, the adoption of spatially explicit distance sampling models to estimate tortoise density expands the suite of metrics defining site characteristics that can be effectively incorporated into models, such as the Normalized Difference Vegetation Index (NDVI) and distance to specific landscape features (e.g., wetlands, roadways). Adoption of spatially explicit distance sampling models may provide greater insight into the spatial processes governing tortoise density, ultimately increasing our understanding of tortoise ecology.

The objectives of this research were to:

1. Develop a spatially explicit distance sampling model to estimate tortoise density and identify habitat associations (Chapter 2)
2. Document adult tortoise resource selection (Chapter 3)
3. Identify vertebrate burrow commensals using abandoned, active, and inactive tortoise burrows within a private, working forest landscape (Chapter 4)

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CHAPTER 2

ESTIMATING GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*) DENSITY WITHIN A PRIVATE, WORKING FOREST LANDSCAPE USING A SPATIALY EXPLICIT DISTANCE SAMPLING MODEL[1]

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Abstract

The gopher tortoise (*Gopherus polyphemus*) is an ecologically important species of the southeastern United States and accurate estimates of density are crucial for monitoring population status and recovery progress. Only recently have robust methods, such as line transect distance sampling, been employed to estimate density across the species' range. Although the use of these methods has produced more robust estimates of density, these methods have limited model covariates to those measured at the plot level. Adoption of spatially explicit distance sampling models may provide greater insight into the spatial processes governing tortoise density, ultimately increasing our understanding of tortoise ecology. Therefore, we conducted line transect distance sampling and used a spatially explicit distance sampling model to estimate abandoned and active tortoise burrow density within a private, working forest landscape located in the Upper Coastal Plain ecoregion of Georgia, USA. We estimated a density of 0.002 burrows/10m^2 (credible interval [CI]= 0.001 – 0.004) and 0.003 burrows/10m^2 (CI = 0.001 – 0.005) for abandoned and active burrows, respectively. We estimated a detection probability of 0.70 (CI = 0.61 – 0.81) and 0.64 (CI = 0.54 – 0.75) for abandoned and active burrows, respectively. We estimated greater densities of active burrows within suitable tortoise soils (e.g., well-drained, sandy) and proximate to early successional stands and forest roads. We estimated greater densities of abandoned burrows within suitable tortoise soils and proximate to pine stands experiencing canopy closure and dense understory conditions. Our results highlight the importance of forest stands characterized by early successional vegetation and forest roads in supporting tortoise populations within a private, working forest landscape. Furthermore, our study demonstrates the ability of spatially explicit distance sampling models to identify the factors affecting tortoise density within these landscapes.

Key words: Gopher tortoise, *Gopherus polyphemus*, *Pinus* spp., density, spatially explicit, distance sampling

1. Introduction

The gopher tortoise (*Gopherus polyphemus*; hereafter, tortoise) is an ecologically important species endemic to the Coastal Plain ecoregion of the southeastern United States (e.g., Young and Goff 1939, Lips 1991, Kinlaw and Grasmueck 2012, Dziadzio and Smith 2016, Potash et al. 2020). Within the last 100 years, tortoise populations have experienced population declines, with these declines attributed to habitat loss (e.g., conversion to agriculture and agroforestry), fragmentation, and degradation (e.g., suppression of natural disturbance regimes), disease, and human exploitation (e.g., Hermann et al. 2002, McCoy et al. 2006, Berish and Leone 2014). In response to these long-term population declines, tortoise populations west of the Mobile and Tombigbee Rivers in Alabama, Mississippi, and Louisiana, USA were listed as threatened under the federal Endangered Species Act (U.S. Fish and Wildlife Service 1987). Tortoise populations east of these river systems in Alabama, Florida, Georgia, and South Carolina, USA were designated as a candidate species (U.S. Fish and Wildlife Service 2011). Uncertainty regarding population status and a recent proposal to reevaluate the species' designation (i.e., threatened) by the United States Fish and Wildlife Service has stimulated research aimed at identifying tortoise population demographics and viability, movement patterns, and habitat associations throughout its range (e.g., Greene et al. 2019, Duffie 2020, Greene et al. 2020, Folt et al. 2021).

Estimates of tortoise density are fundamental for monitoring population status and recovery progress and identifying important habitat associations and landscape-scale influences on populations. Historically, burrow counts were used to estimate tortoise density; however, this method relies on a burrow-to-tortoise correction factor and assumes that all burrows were detected, resulting in questionable results (Smith et al. 2009). As an alternative, line transect distance sampling has been adopted as a method to estimate and monitor tortoise population sizes. Line transect distance sampling provides statistically robust estimates of tortoise burrow density and detection probability, without relying on the assumption that tortoise burrows are uniformly or independently distributed in space or that all burrows are detected (Nomani et al. 2008, Smith et al. 2009, Stober and Smith 2010, Castellon et al. 2015, Gaya 2019, Duffie 2020). Line transect distance sampling allows for population inferences to be made when the units of interest (e.g., tortoise burrows) are not detected (Buckland et al. 2001). Imperfect detection is accounted for by modeling detection probability as a function of perpendicular distance from the transect line (Buckland et al. 2001). Therefore, the use of line transect distance sampling allows for relatively precise and robust estimates of tortoise density in a cost and time effective manner compared to other tortoise survey techniques, such as total counts or sample counts (Nomani et al. 2008, Smith et al. 2009, Castellon et al. 2015).

Conventional distance sampling methods rely on plot-level covariates (e.g., vegetation structure and composition) to explain spatial variation in tortoise density (Nomani et al. 2008, Smith et al. 2009, Stober and Smith 2010, Castellon et al. 2015, Gaya 2019, Duffie 2020). Given that sampling grain has been shown to influence relationships between tortoises and vegetation conditions (e.g., canopy cover, groundcover), it may be advantageous to adopt spatially explicit models that can capture variation in tortoise density within and among sampled plots (Catano et al. 2014, Mizel et al. 2018). Furthermore, the adoption of spatially explicit distance sampling models to estimate tortoise density expands the suite of metrics defining site characteristics that can be effectively incorporated into models, such as the Normalized Difference Vegetation Index (NDVI) and distance to specific landscape features (e.g., wetlands, roadways). For example, permanently open areas, such as utility rights-of-way and roadways, are known to be attractive to tortoises; however, conventional distance sampling approaches are unable to model the influence these landscape features may have on tortoise density in a meaningful way (Wigley et al. 2012, Rautsaw et al. 2018, Duffie 2020, Greene et al. 2020, Marshall, University of Georgia, unpublished data). Using conventional distance sampling approaches would require distance to permanently open areas to be averaged over all burrows detected within a sampling plot. This becomes problematic when no burrow detections occur in a sampling plot, resulting in distance to permanently open areas being 0 or null. In either scenario, these inputs (e.g., null values) can be difficult for conventional distance sampling models to incorporate. Adoption of spatially explicit distance sampling models may provide greater insight into the spatial processes governing tortoise density, ultimately increasing our understanding of tortoise ecology.

Commensurate with the need to adopt spatially explicit distance sampling models to estimate tortoise density, is the need to understand tortoise ecology within private, working forest landscapes (Greene et al. 2020). Tortoises are known to inhabit and persist within these forests warranting their integration into tortoise conservation strategies (Diemer 1992, Berish and Moore 1993, Aresco and Guyer 1999, Jones and Dorr 2004, Diemer Berish et al. 2012, Wigley et al. 2012, Duffie 2020). However, this can be difficult, as there is an incomplete understanding of how tortoises interact with these landscapes (Greene et al. 2020). Of the existing literature, many do not reflect current forest management practices (e.g., chemical site preparation, thinning, forest certification programs etc.) and, thus, may not adequately reflect the ability of private, working forest landscapes to support tortoise populations (Green et al. 2019, Greene et al. 2020, Duffie 2020). This necessitates a reevaluation of these forests under contemporary management practices to identify and understand tortoise habitat associations within these landscapes.

The objectives of our study were to 1) develop a spatially explicit distance sampling model and 2) use the model to estimate abandoned and active tortoise burrow density and evaluate associations between density and edaphic (e.g., soil characteristics, elevation) and stand structural conditions (e.g., canopy cover) present within planted loblolly pine (*Pinus taeda*) stands. Based on prior studies, we predicted that active burrow density would be greatest proximate to forest roads and in early successional stands characterized by sparse canopy cover and abundant herbaceous groundcover. We predicted that abandoned burrow density would increase proximate to forest roads and stands characterized by closed canopy and dense understory (e.g., shrub encroachment) conditions. We expected both active and abandoned burrow density to further increase in forest stands containing elevated areas of suitable tortoise soils (e.g., well-drained, sandy soil).

2. Study Area

Our study was conducted within a private, working forest landscape located in the Upper Coastal Plain ecoregion of Georgia, USA. The site was 32.44 km^2 and consisted predominantly of managed loblolly pine planted in even-aged stands (22.91 km^2), with adjacent stands differing in edaphic (e.g., elevation, soil characteristics) and vegetation conditions (e.g., understory composition and density, canopy cover) because of the timing of forest management (e.g., stand establishment, timber harvest, mid-rotational thinning). Managed pine stands were interspersed with streamside management zones and hardwood areas (5.49 km^2), roads (paved and unpaved; 0.78 km^2), non-forest areas (e.g., wildlife openings, food plots; 0.09 km^2), and utility rights-of-way (0.39 km^2). Lands surrounding our study area consisted of agricultural fields, loblolly pine stands, suburban and rural development, and pine landscapes not managed primarily for timber production. The climate was subtropical with a mean annual temperature of 18.5° C and mean annual precipitation of 130 cm (National Oceanic and Atmospheric Administration 2021). Elevation ranged from 13 to 27 m above sea level, with slopes ranging from 0 to 17.35º.

3. Methods

We conducted line transect distance sampling to estimate abandoned and active gopher tortoise burrow density. We randomly selected 65 forest stands across our study site and placed an 800 m transect within each stand, with the transect split into segments (averaged 4-200 m segments) depending on the shape of the surveyed forest stand and separated by > 25m. Our main objective was to evaluate associations between burrow density and forest stand conditions (e.g., vegetation, edaphic), therefore, transects were restricted to forest stands and did not extend into non-commercial pine areas (e.g., utility rights-of-way, streamside management zone) present within our study site. However, survey transects did extend from adjacent forest roads into stand interiors to quantify the relationship between burrow density and forest roads. A single observer navigated transects with a GPS unit and recorded all burrows detected. The observer measured perpendicular distance of the burrow to the transect, recorded coordinates of each burrow, marked the burrow location with flagging, and classified burrows as active (half-moon shaped opening with indications of recent use) or abandoned (burrow opening collapsed or shape has been altered [no longer roughly shell shaped]; Stober and Smith 2010, Wigley et al. 2012). We then used a fiber optic camera to scope burrows to determine tortoise occupancy, with burrows further classified as occupied, unoccupied, or unable to determine occupancy (i.e., camera could not scope entirety of burrow). Burrow classification (i.e., active or abandoned) was solely based on the physical appearance (e.g., recent use, half-moon shaped) of the burrow and not the presence or absence of a tortoise. We also measured the width and height of burrows and categorized them into an age range based on width (juvenile: 6-10 cm, subadult: 11-15 cm, and adult: >15 cm; Alford 1980, Doonan and Stout 1994). All research was conducted under the University of Georgia Institutional Animal Care and Use Committee (IACUC) protocol A2018 01-018-Y3-A0.

4. Statistical Analysis

We derived most model covariates from national environmental databases (e.g., United States Geologic Survey Digital Elevation Models, Natural Resources Conservation Services [NRCS] Web Soil Survey, etc.), with all data collected at a 10m resolution. From these databases, we obtained measures of elevation, slope, and soil suitability. Soil suitability for tortoises was taken directly from the NRCS Web Soil Survey custom soil resource report for the area of interest (Soil Survey Staff 2020). The report categorized soils as highly suitable or unsuitable for tortoises, with these categories based on soil criteria determined to aid in tortoise burrow excavation and preservation (Soil Survey Staff 2020). Soil criteria included texture, percent coarse fragments, depth to a restrictive layer or a layer with a clay component comprising 35% of the profile, flooding frequency, slope, and depth to seasonal high-water table (Soil Survey Staff 2020). Generally, suitable soils exhibit conditions that aid in burrow construction (e.g., high sand component, well drained) and preservation (e.g., low frequency of flooding) whereas unsuitable soils impede burrow construction (e.g., high clay component) or preservation (e.g., high flooding frequency). We used stand classification (i.e., pine class 0-3 years, 4-7 years, 8-13 years, 14-20 years, 21-31 years), which is based on stand age in years, as a proxy for vegetation conditions (e.g., canopy cover, ground cover), as these classes were shown to encapsulate differences in vegetation structural conditions across planted loblolly pine stands in Mississippi (Foggia 2015; Table 2.1). Furthermore, stand class can be related to forest management activities (e.g., thinning, final harvest) and is a metric more easily interpreted by forest managers. We used distance (meters) to each pine class as a model covariate to improve interpretability.

We built a hierarchical spatial distance sampling model in JAGS within R to estimate tortoise density following the methods of Mizel et al. (2018; R Core Team 2020). We modified the model presented in Mizel et al. (2018) by removing multiple visits and the temporary emigration component (i.e., availability) as these did not apply to our study. Surveyed transects were converted into pixel grids, with pixel grids discretized at a 10 m resolution resulting in an average of 345 pixels per transect. Burrow observations were assigned to the nearest pixel centroid. Pixel centroids were also used to extract and store environmental data (e.g., elevation, soil suitability) associated with the surveyed site. We specified the model for the population point intensity as:

$$\log(\lambda_{ij}) = \beta_0 + \beta_1 x_{1ij} \ldots + \beta_n x_{nij},$$

where *i* represents each pixel and *j* each transect. We used a half-normal detection function:

$$\pi_{ij} = \exp\left(-\frac{d_{i,j}^2}{2\sigma^2}\right),$$

where *d* is the distance from the pixel centroid to the surveyed transect and σ is the scale parameter of the detection function. The observation model consisted of a multinomial (the number of individuals/objects observed in a pixel) and a binomial (observed counts) component:

$$y_{ij} | n_j \sim Multinomial(n_j, \pi_{i,j}^c)$$

$$n_j \sim Binomial(N_j, 1 - \pi_j).$$

We used Markov chain Monte Carlo (MCMC) methods to estimate the posterior distributions of each model covariate. Model covariates included soil suitability, elevation, slope, distance to stand classification (e.g., pine 0-3 years), and distance to forest roads as a linear and quadratic term. All continuous covariates (e.g., elevation) were standardized in R prior to analysis as multiple covariates were collected across different scales (R Core Team 2020). Soil suitability was converted to a set of dummy variables (i.e., columns of 0s and 1s) representing each level (e.g., unsuitable) to aid in model interpretation. We ran 3 chains using semi-informative (i.e., sigma) and vague priors for 2500 iterations after a burn-in of 10 iterations and an adaptive phase of 1000 iterations. We evaluated model convergence by visual inspection of the MCMC chains and using the Gelman-Rubin convergence statistic ($\hat{R}$). We visually evaluated the size and significance of model covariate effects using plots of posterior estimates and generated predictions for model covariates across the range of values present within our study site. We also used the "calc" function (raster package) in R to predict abandoned and active burrow density and abundance across all forest stands within our study site (R Core Team 2020).

5. Results

We detected 112 unique burrows across the 65 surveyed transects, with 62 burrows classified as active and 50 as abandoned. We observed tortoises in 37 (33.03%) of the 112 scoped burrows, with 35 (31.3%) tortoises detected in active and 2 (1.79%) in abandoned burrows. Occupancy status could not be determined for 3 (2.68%) burrows as we were unable to completely scope them (e.g., blocked by debris, flooded). Burrow width ranged from 3.81 – 53.34 cm (mean ± standard deviation; 30.23 ± 7.82 cm) and burrow height ranged from 2.54 – 35.56 cm (17.31 ±

4.05 cm). Mean and standard deviation of active and abandoned burrow width was 31.52 ± 7.61 cm and 28.62 ± 7.85 cm, respectively. Mean and standard deviation of active and abandoned burrow height was 17.43 ± 3.95 cm and 17.17 ± 4.20 cm, respectively. Based on burrow width measurements, we detected a total of 108 adult burrows (59 active and 49 abandoned), three subadult burrows (two active and one abandoned), and one juvenile burrow (active).

We estimated a density of 0.002 burrows/10m^2 (credible interval [CI]= 0.001 – 0.004) and 0.003 burrows/10m^2 (CI = 0.001 – 0.005) for abandoned and active burrows, respectively. Abandoned gopher tortoise burrow density was influenced by soil suitability and distance to stands classified as pine 8-13 years, with a lower density of burrows estimated \ proximate to forest stands classified as pine 8-13 years and on unsuitable tortoise soils (Figure 2.1 and 2.4). Abandoned burrow density did not differ across measures of distance to forest roads, elevation, slope, and pine 0-3 years, 4-7 years, and 21-31 years (Figure 2.1). Active burrow density was influenced by distance to forest roads, distance to pine 0-3 years, and soil suitability (Figure 2.1). Active burrow density increased within areas exhibiting suitable tortoise soils and as distance to early successional stands (pine class 0-3 years) and forest roads (Figures 2.2 and 2.3). Density of active burrows did not differ across measured values of slope, elevation, and distance to pine 4-7 years, 8-13 years, and 21-31 years (Figure 2.1). We estimated a detection probability of 0.70 (CI = 0.61 – 0.81) and 0.64 (CI = 0.54 – 0.75) for abandoned and active burrows, respectively. We estimated that the area surveyed (2.23km^2) contained 71.05 (CI = 59.00 – 88.00; 0.32 burrows/ha) abandoned and 97.66 (CI = 79.00 – 121.00; 0.44 burrows/ha) active burrows. Furthermore, we estimated a total population of 389 (0.15 tortoises/ha) tortoises across planted pine stands (25.70km^2) available within the surveyed private, working forest (Figures 2.4 and 2.5).

6. Discussion

The strongest predictor of abandoned burrow density was soil suitability, whereas the strongest predictor of active burrow density was distance to pine stands characterized by early successional vegetation (i.e., abundant herbaceous groundcover, sparse canopy cover; Table 2.1). Abandoned and active burrow densities were influenced by soil suitability, with both burrow classifications having greater densities in areas exhibiting suitable tortoise soils (e.g., well-drained, sandy). As expected, active burrow density was influenced by vegetation structural conditions present within forest stands. Density of active burrows was greater proximate to pine stands (i.e., pine 0-3 years) characterized by sparse forest canopy cover and herbaceous groundcover (Table 2.1). Furthermore, and as predicted, active burrow density increased proximate to forest roads. Abandoned burrow density increased proximate to forest stands classified as pine 8-13 years. However, and contrary to our initial prediction, abandoned burrow density did not increase within old growth forest stands characterized by closed canopy conditions (e.g., pine 21+; Table 2.1). Furthermore, abandoned burrow density did not differ in relation to distance to forest roads.

Results from our study are consistent with prior research indicating the importance of soil characteristics to tortoises (e.g., Diemer 1992, Aresco and Guyer 1999, Jones and Dorr 2004, Duffie 2020). Greater densities of abandoned and active burrows within suitable soils were not unexpected, as these soil conditions are conducive to burrow construction (e.g., sandy soil) and preservation (e.g., Jones and Dorr 2004, Kowal et al. 2014, Lau and Dodd 2015, Edwards et al. 2016). However, we did observe both abandoned and active burrows within soils whose profiles consisted of sand, loam, and/or clay, indicating that tortoises may utilize a range of soil conditions (Jones and Dorr 2004, Wigley et al. 2012). Future studies should attempt to incorporate fine scale soil characteristics, such as percent coarse or fine loam, percent clay, and depth to water table, in order to gain greater insight into how these factors influence tortoise density within private, working forest landscapes.

Vegetation conditions have also been identified as an important factor governing the distribution and density of tortoises within pine production forests (Jones and Dorr 2004, Wigley et al. 2012, Duffie 2020). Generally, tortoises are distributed within pine stands characterized by early successional vegetation conditions (e.g., sparse canopy cover, abundant herbaceous groundcover), such as recently harvested or thinned stands, and avoid stands experiencing greater canopy closure and reductions in herbaceous groundcover (Berish and Moore 1993, Jones and Dorr 2004, Wigley et al. 2012, Greene et al. 2019, Duffie 2020, Greene et al. 2020). Consistent with previous research, we estimated greater densities of active burrows proximate to forest stands characterized by early successional vegetation conditions compared to more mature forest stands characterized by closed canopy conditions (Berish and Moore 1993, Aresco and Guyer 1999, Jones and Dorr 2004). Furthermore, we estimated greater densities of abandoned burrows proximate to stands classified as pine 8-13 years, with these stands characterized by a barren understory with little to no herbaceous vegetation and a closed canopy. We expected greater densities of abandoned burrows in pine 14-20 and 21+ years as these stands are characterized by closed canopy conditions. However, we found that vegetation conditions within these stands had no effect on abandoned burrow density. We hypothesize that this relationship exists not because tortoises inhabit these stands but by the time stands reach these age classes most abandoned burrows have deteriorated to the point where they are no longer considered burrows from a structural standpoint (e.g., collapsed and filled in) or are no longer available for detection (e.g., present but covered in a thick litter layer) during burrow surveys.

Research has shown that permanently open areas, such as roadside verges and utility rights-of-way, may be attractive to gopher tortoises (Berish and Moore 1993, Wigley et al. 2012, Rautsaw et al. 2018, Duffie 2020, Marshall, University of Georgia, unpublished data). Results from our active burrow model are consistent with these findings, indicating that areas proximate to forest roads may provide vegetation conditions preferred by tortoises, such as sparse canopy cover and herbaceous groundcover. It is plausible that the greater density of active burrows adjacent to forest roads is related to the distribution and density of roads within our study site and not to vegetation structural conditions maintained within and along these areas. However, if burrow density was related to the distribution and density of forest roads, we would expect abandoned burrow density to also be greater proximate to these areas. We did not observe this pattern, indicating that tortoises may be actively selecting for areas proximate to forest roads because of the preferred vegetation conditions that are maintained in perpetuity within these areas (Rautsaw et al. 2018, Marshall, University of Georgia, unpublished data). Considering the density of active burrows was greater proximate to forest roads and within areas exhibiting early successional vegetation conditions suggests that tortoises may use forest roads until suitable conditions become available in adjacent forest stands as a result of forest management, such as stand establishment and final harvest (Berish and Moore 1993, Greene et al. 2020, Marshall, University of Georgia, unpublished data). Forest roads and other permanently open areas, such as utility rights-of-way and wildlife food plots, should be further evaluated to gain a better understanding of the role these areas play in supporting tortoise populations (e.g., facilitating among-patch movements) within private, working forest landscapes.

For management purposes, tortoise populations are defined as “minimum viable”, “primary support”, or “secondary support” populations (Gopher Tortoise Council 2014). A minimum viable population consists of 250 adult tortoises with a density of no less than 0.4 tortoises/ha on a site that is at least 1km^2 (Gopher Tortoise Council 2014). A primary support population has between 50-250 adult tortoises, with a secondary support population having <50 adult tortoises (Gopher Tortoise Council 2014). Designation as a primary or secondary support population does not require a population to meet a tortoise density requirement nor does the population have to reside within a site of a specific area (e.g., 0.5km^2). Based on our results, the tortoise population within our study site would be considered a primary support population, as the population meets the minimum requirement for number of adults (n = 389). However, we estimated a density of only 0.15 tortoises/ha within our study site, which is less than the required 0.4 tortoises/ha to be considered a minimum viable population. Our estimates of tortoise density and the designation of the population as a primary support population are consistent with previous studies conducted within private, working forest landscapes (Jones and Dorr 2004, Duffie 2020).

Although the estimated tortoise population within our study site did not meet the requirements of a minimum viable population, we would argue that it may not need to in order to be considered a stable population that can contribute to tortoise conservation efforts. Previous research has shown that tortoise populations consisting of fewer individuals (n = 66) within a smaller geographic area (6.5 ha) have been stable for 3 decades, with populations predicted to persist well into the future (~ 100 years; Folt et al. 2021). This study indicated that stable populations were characterized by having greater female survival and, generally, a greater number of juvenile tortoises (Folt et al. 2021). This indicates that focusing exclusively on attaining a minimum viable population may be ignoring important demographic parameters associated with population stability while also overlooking the potential of smaller populations to contribute to tortoise conservation efforts (Folt et al. 2021). Future research should instead attempt to estimate demographic parameters, such as recruitment, determine if the population of interest is stable, and identify management strategies that increase these parameters. Furthermore, estimates of tortoise populations should attempt to estimate density across age classes (e.g., hatchling, juvenile) as current estimates of density are generally restricted to adults, as minimal data on juvenile and hatchling burrows are included in density estimation models due to low detectability of these burrows across surveyed sites (Jones and Dorr 2004, Wigley et al. 2012, Gaya 2019, Duffie 2020).

Herein, we used a spatially explicit distance sampling model to estimate abandoned and active tortoise burrow density and evaluate relationships between burrow density and edaphic and vegetative structural conditions within a private, working forest landscape. We were able to evaluate covariates, such as distance to forest roads, that have otherwise proved difficult to quantify using standard distance sampling approaches (e.g., Mizel et al. 2018, Duffie 2020). Our results indicate that forest roads and stands characterized by early successional vegetation may interact to support tortoise populations within the surveyed private, working forest landscape. Based on our results, tortoise burrow surveys should not exclude non-pine stand related areas, such as forest roads and utility rights-of-way. Sampling designs should encapsulate all components (e.g., early rotational stands, mature stands, forest roads, utility rights-of-way) of private, working forest landscapes as this will improve our understanding of tortoise habitat associations and better inform management practices aimed at increasing the compatibility of these forests with tortoise conservation.

Acknowledgements

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Tables and Figures

Table 2.1: Means and standard deviations of percent canopy cover, visual obstruction (VO), and percent ground cover by functional group (e.g., grass, forb, shrub) measured across planted loblolly pine (*Pinus taeda*) stands within a private, working forest located in the Upper Coastal Plain ecoregion of Georgia, USA from 2019.

Pine	Canopy	VO	Grass	Forb	Shrub	Litter
0-3	17.32 ± 31.58	14.76 ± 13.47	8.05 ± 6.19	2.65 ± 1.63	1.19 ± 0.80	81.59 ± 26.05
4-7	53.65 ± 25.14	29.24 ± 15.20	9.15 ± 9.21	2.09 ± 1.46	2.57 ± 1.94	93.41 ± 11.42
8-13	99.09 ± NA	6.59 ± NA	1.11 ± NA	0.03 ± NA	0.18 ± NA	100.00 ± NA
14-20	54.61 ± 42.21	16.69 ± 12.82	10.61 ± 12.31	1.84 ± 2.60	2.00 ± 2.39	96.55 ± 6.81
21+	78.97 ± 21.23	17.41 ± 11.90	6.42 ± 10.26	0.63 ± 0.78	1.59 ± 1.22	95.71 ± 13.02

*NA values result from minimal class 8-13 stands available (n = 5) and surveyed (n = 1) within our study site.

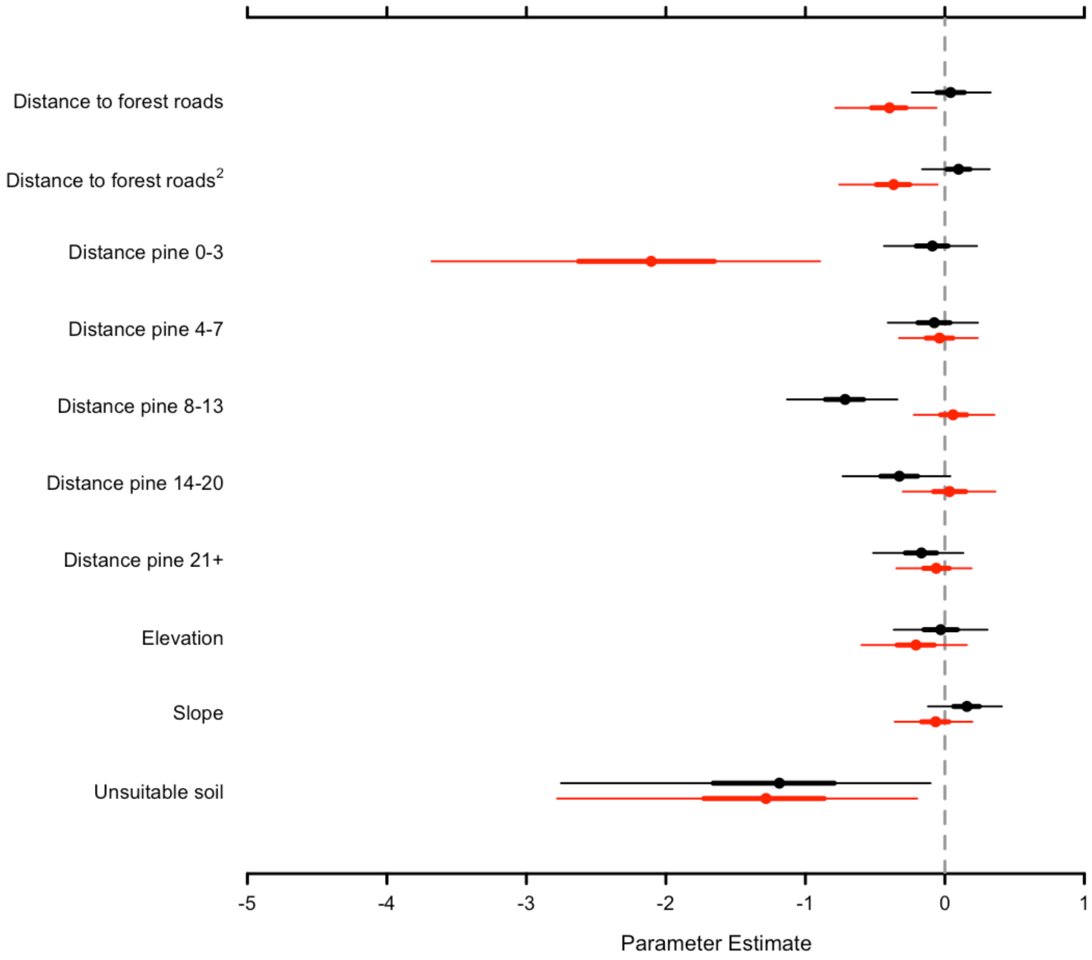

Figure 2.1: Plot of posterior means (points) and 50% (thick lines) and 95% (thin lines) credible intervals for covariates included in a spatially explicit distance sampling model used to estimate abandoned (black lines) and active (red lines) gopher tortoise (*Gopherus polyphemus*) burrow density. Estimates were derived from line transect distance sampling data collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA in 2019.

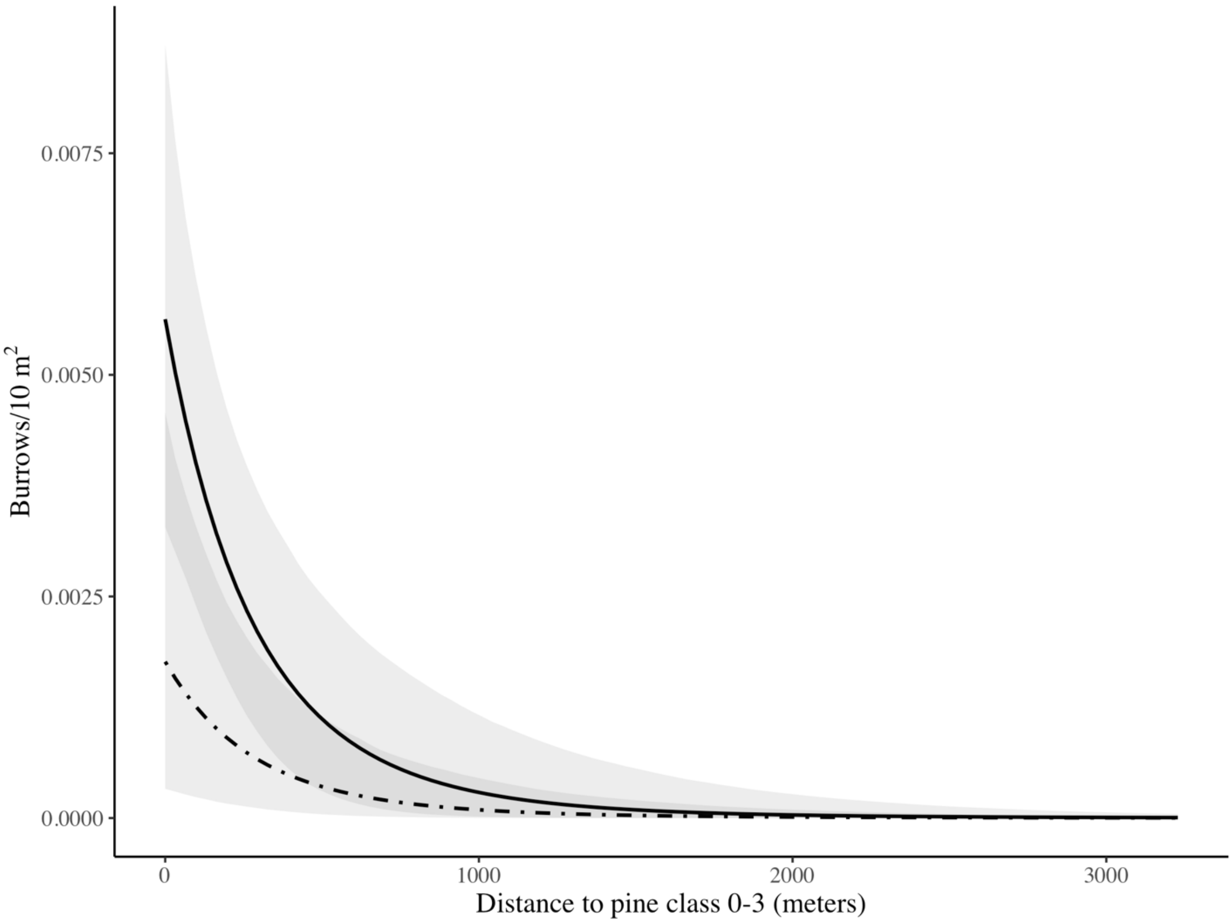

Figure 2.2: Predicted density (with 95% credible intervals) of active gopher tortoises (*Gopherus polyphemus*) burrows within a 10m^2 pixel as a function of distance to forest stands characterized by early successional vegetation (pine class 0-3 years) across suitable (solid line) and unsuitable (dot dashed line) tortoise soils. Estimates were derived from line transect distance sampling data collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA in 2019.

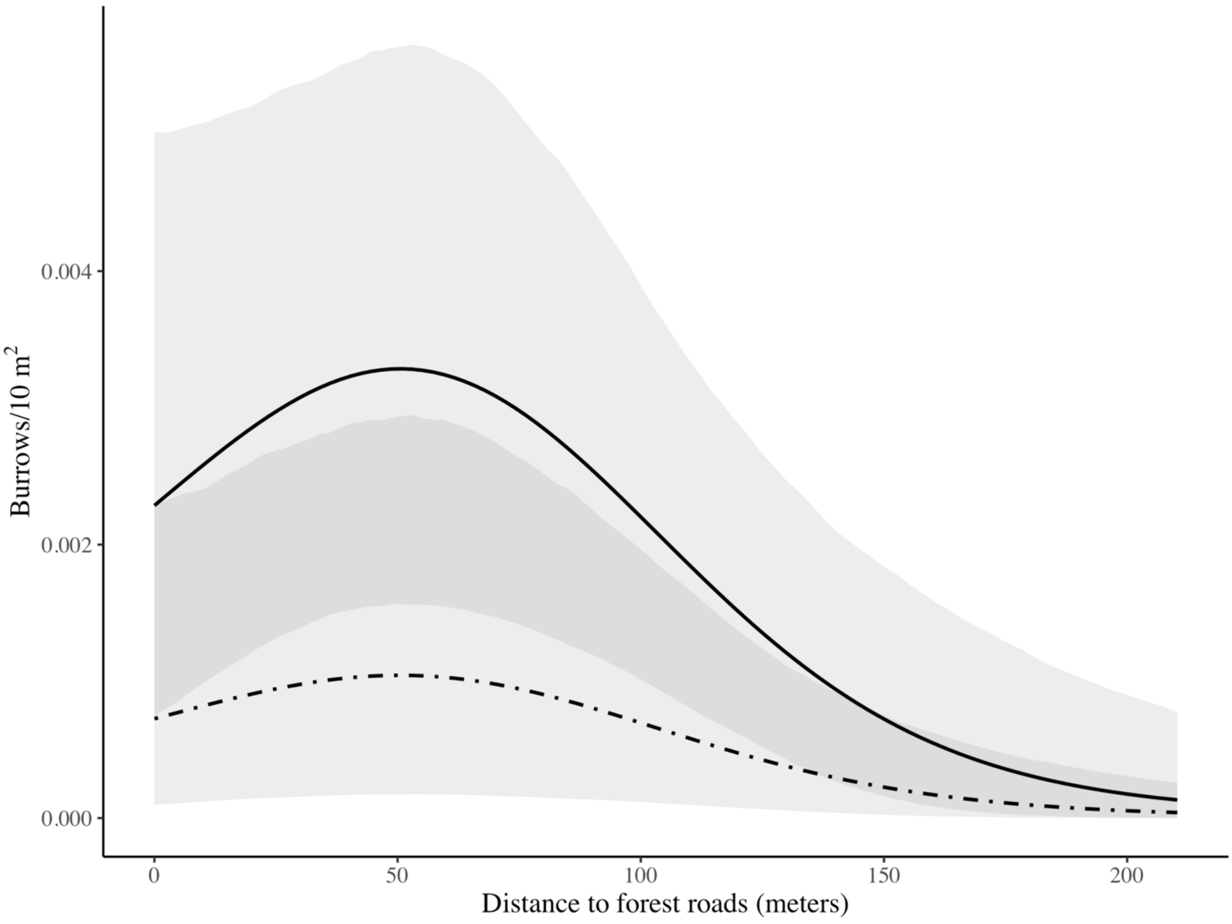

Figure 2.3: Predicted density (with 95% credible intervals) of active gopher tortoises (*Gopherus polyphemus*) burrows within a $10m^2$ pixel as a function of distance to forest roads across suitable (solid line) and unsuitable (dot dashed line) tortoise soils. Estimates were derived from line transect distance sampling data collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA in 2019.

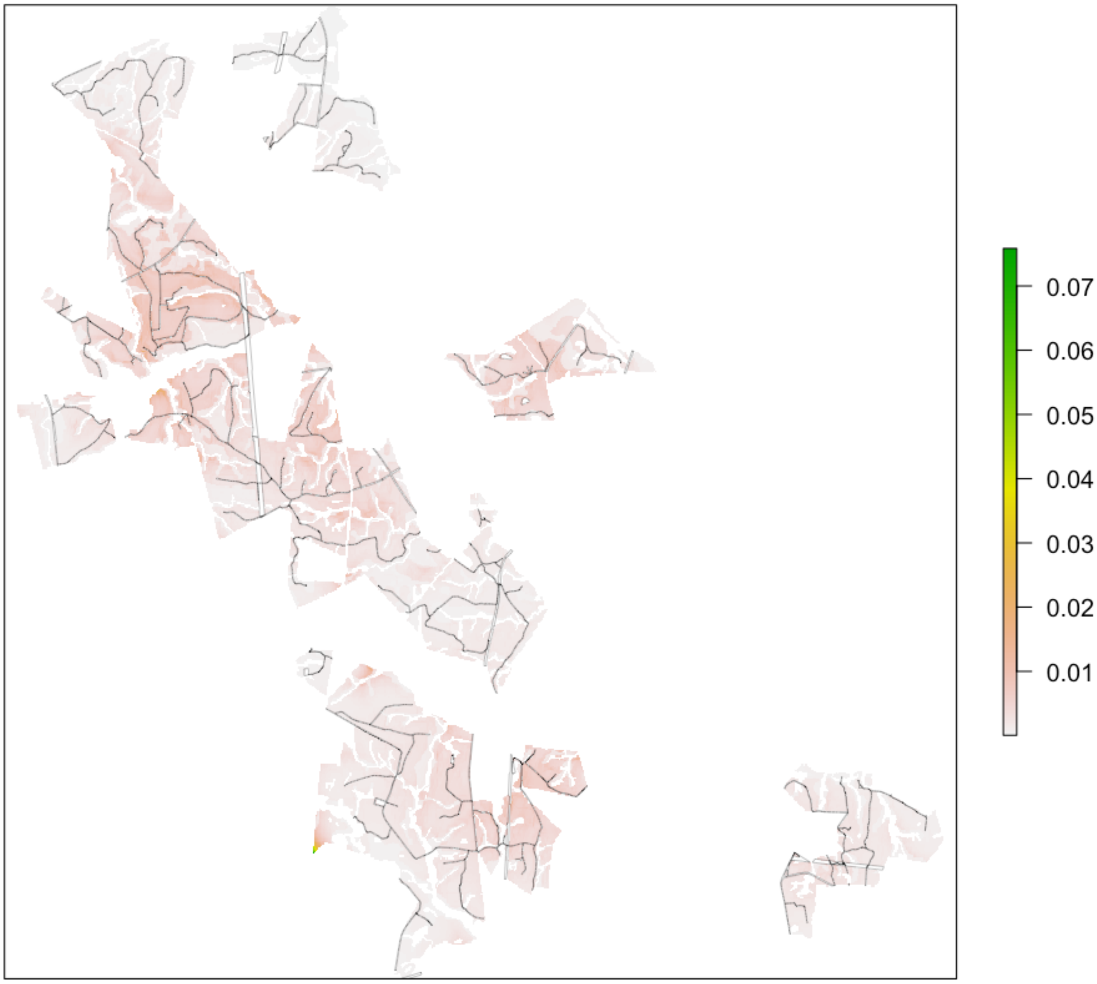

Figure 2.4: Posterior predictions of abandoned gopher tortoise (*Gopherus polyphemus*) burrow density (tortoises/10m^2) across an entire private, working forest landscape. The black lines represent forest roads. Estimates were derived from line transect distance sampling data collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA in 2019.

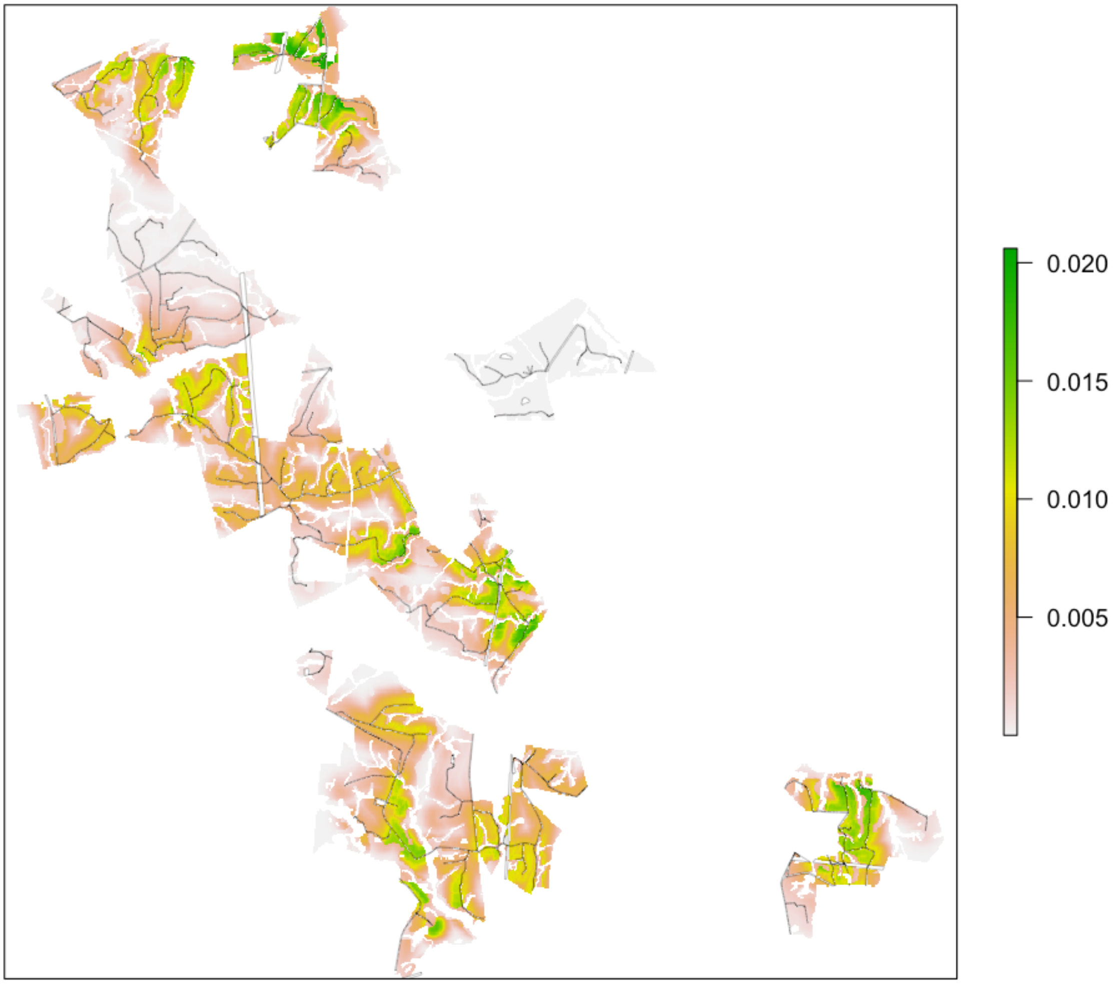

Figure 2.5: Posterior predictions of active gopher tortoise (*Gopherus polyphemus*) burrow density (tortoises/10m^2) across an entire private, working forest landscape. The black lines represent forest roads. Estimates were derived from line transect distance sampling data collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA in 2019.

CHAPTER 3

GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*) RESOURCE SELECTION WITHIIN A PRIVATE, WORKING FOREST LANDSCAPE[2]

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[2] Marshall, C.D., J. A. Martin, A. L. Larsen-Gray, M. J. Chamberlain, J. C. Maerz. To be submitted to *Forest Ecology and Management*.

Abstract

Private, working forest landscapes provide wildlife habitat and understanding how species interact with these landscapes is critical to identifying conservation opportunities. The gopher tortoise (*Gopherus polyphemus*; hereafter, tortoise) is a species endemic to the Coastal Plain ecoregion of the southeastern United States, with private, working pine (*Pinus* spp.) forests encompassing a substantive portion of area within the species' range. Although private, working forests contain tortoises, uncertainty exists as to how tortoises use these landscapes. Specifically, there is limited information regarding tortoise habitat associations within these landscapes relative to current forest management practices. Therefore, we used radio telemetry data from 55 adult tortoises collected over 3 years to estimate resource selection within a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) stands in the Upper Coastal Plain ecoregion of Georgia, USA. Tortoises selected sites proximate to permanently open areas (e.g., roads and utility rights-of-way) and forest stands characterized by early successional vegetation conditions. To a lesser extent, tortoise selected areas of higher elevation and with soils considered suitable for tortoises. We found no strong evidence indicating that forest stands provide greater than 4 years of vegetation conditions (e.g., sparse canopy cover, abundant herbaceous groundcover) preferred by tortoises. Our results suggest that permanently open areas, such as utility rights-of-way and forest roads, and forest stands characterized by early successional vegetation may interact to enable tortoise populations to inhabit and persist within our private, working forest site.

Key words: Gopher tortoise; *Gopherus polyphemus*; resource selection; private, working forests; *Pinus taeda*; loblolly pine; forest management; Georgia

1. Introduction

Private, working forests represent substantial areas of habitat for wildlife and are predicted to become an increasingly important component of species conservation (Knight 1999, Herman et al. 2002, Underwood et al. 2012, Greene et al. 2020*a*). Private forests are a common component of the southeastern United States, encompassing ~85 million hectares (Oswalt et al. 2019). These forests contribute to terrestrial biodiversity via maintenance of forested areas and a diversity of stand and forest types spatially and temporally (e.g., Elmore et al. 2004, Miller et al. 2009, Greene et al. 2016, Demarais et al. 2017). However, contributions of these forests to terrestrial biodiversity are dependent on forest management practices (e.g., rotation length, stand establishment practices, intermediate treatments) and individual species' habitat needs (Miller et al. 2009, Demarais et al. 2017). Forest management on private, working forests often creates a shifting mosaic of vegetation conditions that are appropriate for some wildlife species. However, it is unclear which species can capitalize on the availability of those shifting conditions (Greene et al. 2016, Greene et al. 2019).

The gopher tortoise (*Gopherus polyphemus*; hereafter, tortoise) is a high priority Species of Greatest Conservation Need of the southeastern United States, with private lands encompassing greater than 80% of the species' range (Hermann et al. 2002, Underwood et al. 2012, Greene et al. 2020*b*). This private land designation includes private, working forests that primarily consist of even-aged pine (*Pinus* spp.) stands planted to produce merchantable forest products (e.g., timber, pulp wood, utility poles). Private, working pine forests are ubiquitous across the tortoise's range and tortoise populations are known to inhabit and persist within these landscapes (Aresco and Guyer 1999, Jones and Dorr 2004, Diemer Berish et al. 2012, Wigley et al. 2012, Duffie 2020, Greene et al. 2020*b*). Historically, these forests were generally considered unsuitable for tortoises. However, forest management practices have evolved and more contemporary private, working forest landscapes may provide resources for tortoise populations. Therefore, understanding how tortoises use private, working forests, particularly under contemporary management practices, is important to understanding the compatibility of these forests with tortoise conservation.

Structural conditions within planted pine stands frequently fluctuate because of continuous forest management activities, such as site preparation, stand establishment, thinning, and final harvest. This creates a complex and dynamic mosaic of structural and edaphic conditions across private, working forest landscapes (Miller et al. 2009, Wigley et al. 2012, Greene et al. 2016, Demarais et al. 2017, Greene et al. 2019, Greene et al. 2020*b*). It has been suggested that these shifting conditions can maintain tortoise habitat that is spatially and temporally connected, facilitating among-patch tortoise movements (Greene et al. 2019). That is, as conditions for tortoises deteriorates in one stand (e.g., increasing canopy cover), conversion of adjacent or nearby stands to more open conditions via thinning, final harvest, or other treatments (e.g., prescribed fire, herbicide use) may allow tortoises to move among stands in a manner that can sustain populations long-term. Among stand movements have been documented, although it is unclear if these movements were related to changes in habitat conditions associated with forest management (e.g., stand establishment, thinning, final harvest) or other phenomena (e.g., males searching for females during the breeding season, use of heavy machinery disturbing tortoises; Dimer 1992). Tortoises also may exhibit greater plasticity in habitat associations when inhabiting closed canopy forest stands, albeit at lower densities, with this plasticity potentially contributing to the ability of tortoises to persist within the mosaic of forest stands characteristic of private, working forest landscapes (Wigley et al. 2012).

Despite the potential for private, working forest landscapes to contribute to tortoise conservation, evaluations of tortoise use have generally been limited to public ownership (e.g., military installations, wildlife management areas; Baskaran et al. 2006, Tuberville et al. 2007, Kowal et al. 2014). To date, no study has evaluated tortoise resource selection in a private, working forest landscape under contemporary forest management. Therefore, our objective was to assess adult tortoise resource selection within a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) stands. We predicted that tortoises would be more likely to use areas within forest stands exhibiting sparse forest canopy cover and abundant herbaceous groundcover and proximate to relatively permanent, human-maintained open areas (e.g., forest roads, utility rights-of-way). We also predicted that the likelihood of tortoises using more open canopy forest stands and permanently open areas would further increase if these areas contained upland areas of suitable soils (e.g., well-drained, sandy soils) conducive to burrow construction and growth of herbaceous forage (e.g., forbs, graminoids).

2. Study Area

Our study was conducted within a private, working forest landscape located in the Upper Coastal Plain ecoregion of Georgia, USA. The site was 32.44 km^2 and consisted predominantly of managed loblolly pine planted in even-aged stands (22.91 km^2), with adjacent stands differing in edaphic (e.g., elevation, soil characteristics) and vegetation conditions (e.g., understory composition and density, canopy cover) because of the timing of forest management (e.g., stand establishment, mid-rotational thinning, final harvest). Managed pine stands were interspersed with streamside management zones and hardwood areas (5.49 km^2), roads (paved and unpaved; 0.78 km^2), non-forest areas (e.g., wildlife openings, food plots; 0.09 km^2), and utility rights-of-way (0.39 km^2). Lands surrounding our study area consisted of agricultural fields, loblolly pine stands, suburban and rural development, and pine landscapes not managed primarily for timber production. The climate was subtropical with a mean annual temperature of 18.5° C and mean annual precipitation of 130 cm (National Oceanic and Atmospheric Administration 2021). Elevation ranged from 13 to 27 m above sea level, with slopes ranging from 0 to 17.35º.

3. Methods

We captured tortoises with wire cage traps placed over the entrance of known occupied burrows or opportunistically by hand. For each tortoise, we measured straight-line carapace length (mm) and mass (g), determined sex using visible secondary sexual characteristics, and estimated age by counting scute annuli. We classified tortoises with a carapace length ≥ 220 mm and a conspicuous plastral concavity and/or an elongated gular as male and tortoises with a carapace length ≥ 230 mm and no secondary sexual characteristics as female (Tuberville et al. 2014). We uniquely marked each tortoise on the marginal scutes using a triangular file (Florida Fish and Wildlife Conservation Commission 2008). We considered captured tortoises as adults if they were ≥ 9 years of age (measured using scute annuli) or had a carapace length ≥ 220 mm for males and carapace length ≥ 230 mm for females when age could not be determined due to deterioration of scute annuli. We used epoxy to affix very high frequency (VHF) radio transmitters to the anterior carapace of adult tortoises, with radio transmitters adhered to the anterior carapace to avoid interfering with reproduction or movement in and out of burrows. Radio transmitters weighed less than 1% (< 41 g) of the average weight of an adult tortoise. We monitored tortoises via homing 3 to 5 times per week during the high activity seasons (May-September) of 2018 and 2019, and once per month during 2020. During each tracking event, we recorded date, time, GPS coordinates, location (e.g., burrow, stand, roadway) and behavior if outside of burrow (e.g., moving, foraging). We conducted all research activities under the University of Georgia Institutional Animal Care and Use Committee (IACUC) protocol A2018 01-018-Y3-A0.

4. Statistical Analyses

We investigated second order resource selection of adult tortoises and used an uncorrelated random walk model that pulled from distributions of known step lengths and absolute angles (angle from the horizontal plane [x]) to generate available locations for tortoises. We used available locations derived from the random walk model to compare with actual tortoise locations to determine differential use. Using a random walk model enabled us to mimic tortoise movements and probabilities of those movements occurring to generate random available locations. Other conventional resource selection approaches, such as selecting available locations from within home range boundaries or using buffer distances based on mean or maximum movements, would have dramatically reduced our ability to make inferences regarding tortoise resource selection. Estimated home ranges (≤ 0.5 ha for multiple individuals) and average movements for tortoises were small (mean female movement distance 10 m ± 35 m; mean male movement distance 33 m ± 77 m), so using those areas or distances would restrict potential available locations to areas not indicative of what was reasonably available to tortoises. Conversely, using maximum movement distances (341 m and 734 m for females and males, respectively) as buffers would generate large available areas, but such movements were rare (1 instance of both movements) and would therefore overrepresent area available to a tortoise.

Using the random walk approach did not require us to generate an arbitrary boundary to define availability for tortoises.

We randomly generated 5 starting locations across our study area for each tortoise, resulting in 275 random starting locations. Because our objective was to assess second order resource selection, we did not generate random movement paths from initial tortoise capture locations. From each random starting location, we generated a random walk whose length (number of steps) was dictated by the number of tracking events for each individual tortoise (Hunt 2014). For example, a tortoise that was located 110 times had 5 random walks whose individual lengths were equal to 110 steps. We generated random walks for each tortoise separately, using different distributions of step lengths and absolute angles for female and male tortoises as these movement metrics differed by sex. Generating random walks from distributions of known male and female step lengths and absolute angles allowed us to capture instances of movement and no movement within the model. Using this method, we randomly generated 20,700 available locations to produce an approximately 5:1 ratio of available and used tortoise locations. We selected this ratio of available to used tortoise locations to aid in model convergence (Northrup et al. 2013).

We derived most model covariates from national environmental databases (e.g., United States Geologic Survey Digital Elevation Models, Natural Resources Conservation Services [NRCS] Web Soil Survey, etc.), with all data collected at a 10m resolution. From these databases, we obtained measures of elevation, slope, and soil suitability. Soil suitability for tortoises was taken directly from the NRCS Web Soil Survey custom soil resource report for the area of interest (Soil Survey Staff 2020). The report categorized soils as highly suitable, moderately suitable, less suitable, or unsuitable for tortoises, with these categories based on soil criteria determined to aid in tortoise burrow excavation and preservation (Soil Survey Staff 2020). Soil criteria included texture, percent coarse fragments, depth to a restrictive layer or a layer with a clay component comprising 35% of the profile, flooding frequency, slope, and depth to seasonal high-water table (Soil Survey Staff 2020). Generally, suitable soils exhibit conditions that aid in burrow construction (e.g., high sand component, well drained) and preservation (e.g., low frequency of flooding) whereas unsuitable soils impede burrow construction (e.g., high clay component) or preservation (e.g., high flooding frequency). We used forest stand classification (i.e., pine class 0-3 years, 4-7 years, 8-13 years, 14-20 years, 21-31 years) as a proxy for vegetation conditions (e.g., canopy cover, ground cover), as these classes have been shown to encapsulate differences in vegetation structural conditions across planted loblolly pine stands (Foggia 2015; Table 3.1). Furthermore, forest stand class can be related to forest management activities (e.g., thinning, final harvest) and is a metric more easily interpreted by forest managers. We used distance to each forest class as a model covariate to improve interpretability. We measured distance between forest classes and permanently open areas, and used and available locations, using GIS software (QGIS Development Team 2020).

We fit a resource selection function in R (statistical package version 4.0.3) with a logit link fitted in JAGS to estimate the probability of use for adult tortoises (Plummer 2003, R Core Team 2020). We included individual-specific intercepts (β_{0j}; where j = individual) to account for unequal sample sizes across individuals (Gillies et al. 2006, Muff et al. 2020). The resource selection function was as follows:

$$logit(x_i) = \beta_{0j} + \beta_1 x_1 + \cdots + \beta_n x_n.$$

Covariates ($x_1 \ldots x_n$) included soil suitability (high, moderate, less, and unsuitable), distance to forest stand classes, elevation, slope, and distance to permanently open areas. We did not include paved roads in our designation of permanently open areas as these roads were few in number (*n* = 2) and located at significant distance from used and available locations. We standardized all continuous covariates (e.g., distance to permanently open areas, elevation) in R prior to analysis as multiple covariates were collected across different scales (R Core Team 2020). We converted soil suitability to a set of dummy variables (i.e., columns of 0s and 1s) representing each level of suitability (highly suitable, moderately suitable, less suitable, and unsuitable) to aid in model interpretation. We used Markov chain Monte Carlo (MCMC) methods to estimate the posterior distributions of each model parameter. We ran 3 chains using non-informative priors for 2500 iterations after a burn-in of 10 iterations and an adaptive phase of 1200 iterations. We evaluated model convergence by visual inspection of the MCMC chains and using the Gelman-Rubin convergence statistic ($\hat{R}$). We visually evaluated the size and significance of model covariate effects using density plots of posterior estimates and generated prediction intervals for model covariates across the range of values present within our study area.

We then converted model covariates to odds ratios (OR) by exponentiating the estimate of the covariate. We scaled the odds ratios based on the standard deviation of the model covariate, with all continuous model covariates scaled with a mean of 0 and standard deviation of 1 (Table 3.2). Thus, if elevation had a standard deviation of 8.49 m and an OR of 3.15, we interpreted the OR as the odds of tortoise use increasing 3.15 times for each 8.49 m increase in elevation. If elevation had an estimated OR of 1.34, then we interpreted the OR as the odds of tortoise use increasing by 1.34 (34%) for each 8.49 m increase in elevation. If elevation had a negative effect on tortoise use and an estimated OR of 1.34, then the odd of tortoise use would 1.34 times less likely for each 8.49 m increase in elevation.

5. Results

We captured and affixed radio transmitters to 58 adult tortoises (22 females and 36 males) during the high activity seasons (May – August) of 2018 and 2019. Mean and standard deviation of the distance a tortoise was captured from a permanently open area was 31.24 ± 64.14 m. Mean and standard deviation of female weight and straight-line carapace length were 5.27 ± 1.40 kg and 30.16 ± 6.98 cm, respectively. Of the 58 radio-tagged tortoises, we successfully monitored 55 (21 females and 34 males), resulting in 4,348 tracking events, with a mean of 79.05 ± 32.97 tracking events per tortoise. Across all 4,348 tracking events, we observed tortoises within a burrow 94% of the time. The remaining 6% of tortoise observations were within permanently open areas (1%), planted pine stands (2%), or unknown locations (4%; e.g., private property). Of the 133 (3%) observations of tortoises outside of burrows (i.e., within permanently open areas or forest stands), 32 (24%) were of individuals foraging and 101 (76%) were of individuals moving. 13 (41%) foraging observations were within permanently open areas, with the remaining occurring in pine class 0-3 years (*n* = 8; 25%), pine class 4-7 years (*n* = 5; 16%), pine class 14-20 years (*n* = 4; 12%), and pine class 21-31 (*n* = 2; 6%). 53 (52%) observations of individuals moving occurred within permanently open areas, with the remaining occurring in pine class 0-3 years (*n* = 11; 11%), pine class 4-7 years (*n* = 7; 7%), pine class 14-20 years (*n* = 11; 11%), and pine class 21-31 years (*n* = 19; 19%). Tortoises observed foraging or moving within forest stands were, on average (± standard deviation), 31.18 ± 29.86 m and 33.4 ± 36.79 m from permanently open areas, respectively.

Tortoise resource selection was influenced by soil suitability, distance to permanently open areas, distance to forest classes, and elevation. Tortoises exhibited no preference for the range of slopes available within our study area. Suitable soils, elevation, distance to hardwood areas (e.g., streamside management zones) and distance to certain forest classes (e.g., pine class 4-7 years) had comparable effects on tortoise selection (Figure 3.1). However, effects of these covariates on tortoise selection were moderate in comparison to effects of distance to permanently open areas and distance to pine class 0-3 years (Figure 3.1). Tortoises selected for highly suitable soils with a greater probability than moderately (OR = 1.67, 95% credible interval (CRI) = 1.46 – 1.90), less (OR = 1.62, CRI = 1.42 – 1.85), and unsuitable (OR = 2.31, CRI = 1.99 – 2.68) soils (Figure 3.1). Moderately and less suitable soils were selected for similarly, whereas unsuitable soils had the lowest probability of use (Figure 3.1). Tortoise use increased at higher elevations (OR = 2.36, CRI = 2.20 – 2.53; Figure 3.2) and proximate to permanently open areas (OR = 7.84, CRI = 7.14 – 8.61; Figure 3.3). Tortoise use increased as distance to pine class 0-3 years (OR = 4.78, CRI = 4.25 – 5.40; Figure 3.4), pine class 4-7 years (OR = 1.26, CRI = 1.19 – 1.33), pine class 8-13 years (OR = 1.32, CRI = 1.24 – 1.41), and pine class 14-20 years (OR = 1.35, CRI = 1.25 – 1.42) decreased, whereas tortoise use declined as distance to pine class 21-31 years (OR = 1.32, CRI = 1.24 – 1.41) and hardwood areas (OR = 1.08, CRI = 1.01 – 1.15) decreased.

6. Discussion

The strongest predictors of resource selection by tortoises were proximity to permanently open areas, specifically a utility right-of-way and areas adjacent to unpaved forest roads, and proximity to forest stands characterized by early successional vegetation conditions (i.e., forest class pine 0-3 years; Table 3.1). As expected, tortoises selected higher elevation areas of suitable soils and selected against mature forest stands (i.e., forest class pine 21-31 years) and hardwood areas (e.g., streamside management zones). However, selection for these factors was relatively modest compared to selection for permanently open areas and early successional forest stands. Selection for suitable elevated, well-drained, and sandy soil was consistent with prior research demonstrating the importance of edaphic factors to tortoise density and habitat use (e.g., Diemer 1992, Aresco and Guyer 1999, Jones and Dorr 2004, Baskaran et al. 2006, Kowal et al. 2014, Castellon et al. 2020). Although we cannot draw conclusions regarding tortoise foraging habits and movement patterns due to minimal observations of these behaviors, the few observations collected in our study suggest that tortoises may use permanently open areas as foraging locations and movement corridors (Rautsaw et al. 2018). Furthermore, tortoises may also be using stand edges and not stand interiors for foraging and movement based on our observations of these behaviors proximate to permanently open areas. Future studies should attempt to evaluate tortoise preferences for foraging areas and identify movement corridors within private, working forest landscapes.

Tortoises in our study were generally captured proximate to permanently open areas (mean distance and standard deviation = 31.23 ± 64.14 m, range = 0 – 438 m). This has the potential to bias tortoise selection towards these areas. However, tortoise burrow surveys conducted within our study site indicate that burrows were generally distributed along forest roads (mean distance and standard deviation = 59.69 ± 36.75 m) and uncommon within forest stand interiors (Marshall, University of Georgia, unpublished data). Furthermore, this study did not survey other permanently open features, such as utility rights-of-way, present within our study site, suggesting that mean distance of burrows to these features may be less than indicated by this study (Marshall, University of Georgia, unpublished data). This pattern has also been observed in previous tortoise burrow surveys conducted within other contemporary private, working forest landscapes (Wigley et al. 2012, Duffie 2020). These findings support that our tortoise capture locations were representative of the distribution of the tortoise population within our study site.

Based on our results, tortoises preferred permanently open areas and forest stands characterized by early successional vegetation within our study site. Forest stands within our study site provided early successional vegetation conditions (e.g., sparse canopy cover, abundant herbaceous understory) consistent with tortoise habitat post-harvest and up to 3 years post stand establishment. Research indicates that pine stands can provide up to 4 – 8 years of additional early successional vegetation conditions because of continuous forest management, such as commercial thinning, prescribed fire, and selective herbicide (Yager et al. 2007, Ashton et al. 2008, Iglay et al. 2014, Greene et al. 2016, Greene et al. 2019). Commercial thinning was conducted at our study site. However, our results do not indicate that tortoises selected for recently thinned stands (thinning generally occurs within stands classified as 14-20 years). This indicates that thinning operations conducted within our study site may not promote vegetation conditions (e.g., sparse canopy cover, herbaceous understory) preferred by tortoises or may be too ephemeral on the landscape for tortoises to exploit. To increase the compatibility of forest stands with tortoise conservation on our study site, we suggest coupling prescribed fire and/or other disturbance regimes with current forest management activities, such as commercial thinning and herbicide application, to promote suitable vegetation conditions over a greater temporal and spatial extent (Yager et al. 2007, Iglay et al. 2014, Ashton et al. 2008).

Permanently open areas, such as forest roads, roadside verges, and utility rights-of-way, are likely attractive to tortoises because of the stable open canopy conditions that allow for abundant growth and persistence of perennial herbaceous groundcover (Wigley et al. 2012, Rautsaw et al. 2018, Duffie 2020, Greene et al. 2020*b*). Permanently open areas are regularly disturbed (e.g., mowing, herbicide application) to reduce woody encroachment that can negatively affect power lines or reduce visibility along roadways. These disturbances may mimic more natural disturbances, such as prescribed fire, that create persistent early successional conditions (e.g., sparse canopy cover, herbaceous understory) preferred by tortoises and sustain higher population densities (Yager et al. 2007, Ashton et al. 2008). This likely explains the preferential selection for locations within and proximate to permanently open areas on our study site. Based on our results, permanently open areas and forest stands characterized by early successional vegetation conditions may complement each other on the landscape and enable tortoises to persist within our study site. As suggested by prior research, tortoises may be using permanently open areas until early successional vegetations conditions become available in adjacent forest stands because of ongoing forest management activities (Diemer 1992, Berish and Moore 1993, Greene et al. 2020*b*).

Herein we identified permanently open areas, such as forest roads and utility rights-of-way, and forest stands characterized by early successional vegetation conditions as important landscape components to adult tortoises within a private, working pine forest. However, it is unclear if and how these areas interact to enable tortoise populations to persist within these forests. Furthermore, studies of tortoise movements have generally been short-term (e.g., 2-3 years), limiting our ability to make inferences about how tortoises move within these landscapes. We have an incomplete understanding of how tortoises locate stands characterized by early successional vegetation conditions (e.g., random movements vs. spatial awareness) and if tortoises use specific areas, such as forest roads, as movement corridors. We also have limited knowledge of tortoise demographic parameters (e.g., adult, juvenile, and nest survival) in general and especially within private, working forest landscapes (e.g., Tripp et al. 2018, Duffie 2020).

Furthermore, we have no information on nest site selection and hatchling and juvenile resource selection within these landscapes even though nest and hatchling and juvenile tortoises have been observed in private, working forest landscapes (Marshall, University of Georgia, unpublished data). Although adult tortoises are persisting within our study area by using permanently open areas and forest stands characterized by early successional vegetation, it is unclear if these areas provide adequate nesting sites or resources required by hatchling and juvenile tortoises. In other words, it is unclear if these areas provide sufficient resources (e.g., nest sites, cover for hatchlings) to facilitate recruitment. Future studies should focus on long-term evaluations of tortoise movements and estimating demographic parameters and resource selection across tortoise age classes to improve our understanding of how permanently open areas and stand vegetation conditions influence tortoise use and population dynamics within contemporary private, working forest landscapes. Results from these studies will provide much needed information that can be used to generate management recommendations that increase the compatibility of private, working forest landscapes with tortoise conservation.

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Tables and Figures

Table 3.1: Means and standard deviations of percent canopy cover, visual obstruction (VO), and ground cover by functional group (e.g., grass, forb, shrub) measured across planted loblolly pine (*Pinus taeda*) stands within a private, working forest located in the Upper Coastal Plain ecoregion of Georgia, USA from 2019. These data were collected from 65 forest stands that were randomly selected to be surveyed for tortoise burrows for a tortoise density study conducted within our study site (Marshall, University of Georgia, unpublished data).

Pine	Canopy	VO	Grass	Forb	Shrub	Litter
0-3	17.32 ± 31.58	14.76 ± 13.47	8.05 ± 6.19	2.65 ± 1.63	1.19 ± 0.80	81.59 ± 26.05
4-7	53.65 ± 25.14	29.24 ± 15.20	9.15 ± 9.21	2.09 ± 1.46	2.57 ± 1.94	93.41 ± 11.42
8-13	99.09 ± NA	6.59 ± NA	1.11 ± NA	0.03 ± NA	0.18 ± NA	100.00 ± NA
14-20	54.61 ± 42.21	16.69 ± 12.82	10.61 ± 12.31	1.84 ± 2.60	2.00 ± 2.39	96.55 ± 6.81
21+	78.97 ± 21.23	17.41 ± 11.90	6.42 ± 10.26	0.63 ± 0.78	1.59 ± 1.22	95.71 ± 13.02

*NA values result from minimal class 8-13 stands available (n = 5) and surveyed (n = 1) within our study site.

Table 3.2: Means and standard deviations for all continuous model covariates included in the gopher tortoise (*Gopherus polyphemus*) resource selection function. We derived estimates from gopher tortoise tracking data collected in planted loblolly pine (*Pinus taeda*) stands located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018 – 2020.

Covariate	Mean ± Standard Deviation
Distance to permanently open areas	90.10 ± 78.08m
Distance to forest class 0-3	454.11 ± 729.57m
Distance to forest class 4-7	574.33 ± 637.07m
Distance to forest class 8-13	1264.30 ± 924.20m
Distance to forest class 14-20	535.13 ± 630.82m
Distance to forest class 21-31	236.23 ± 263.25m
Distance to hardwood areas	87.38 ± 79.98m
Slope	2.48 ± 1.52°
Elevation	65.90 ± 8.57 m

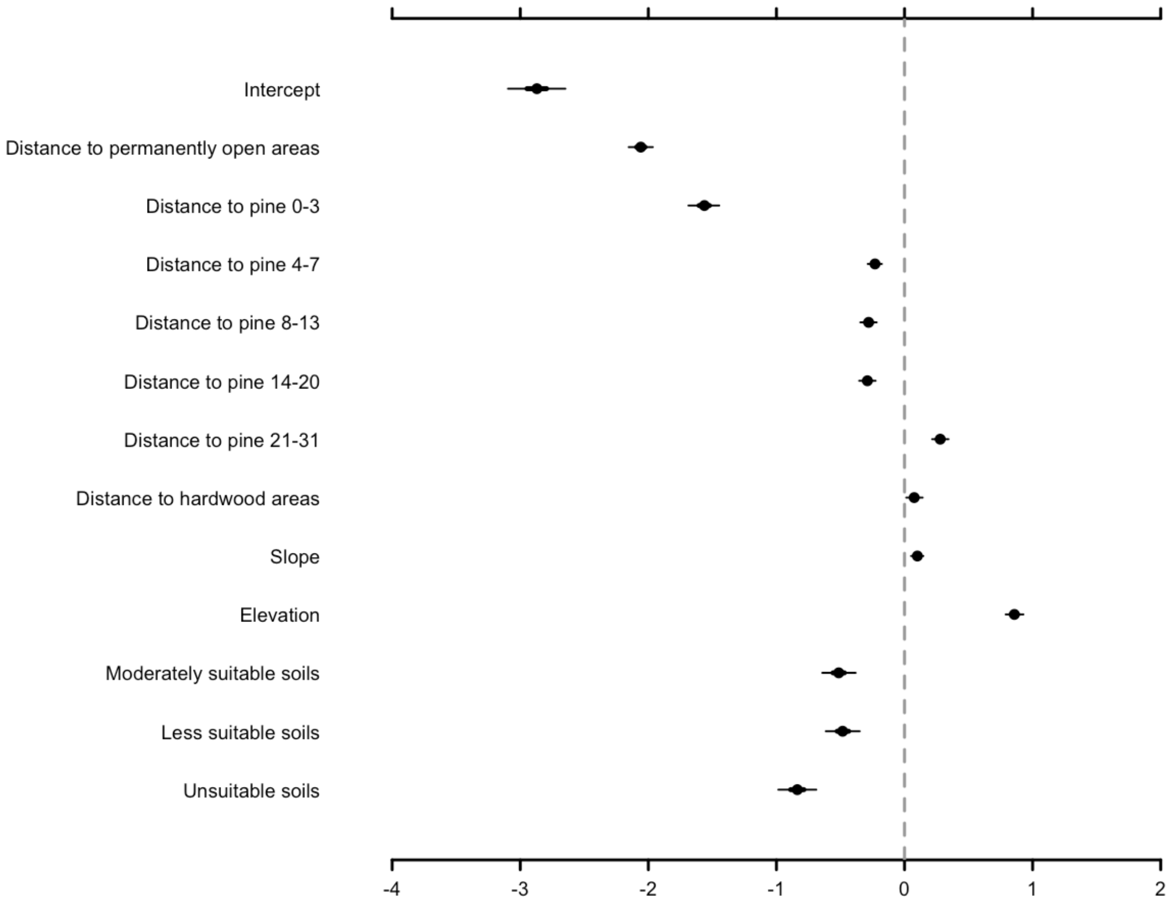

Figure 3.1: Posterior estimates of model covariates (black dot) and 95% credible intervals (black line). Estimates were derived from gopher tortoise (*Gopherus polyphemus*) tracking data collected in a private, working forest dominated by planted loblolly pine (*Pinus taeda*) located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018 – 2020.

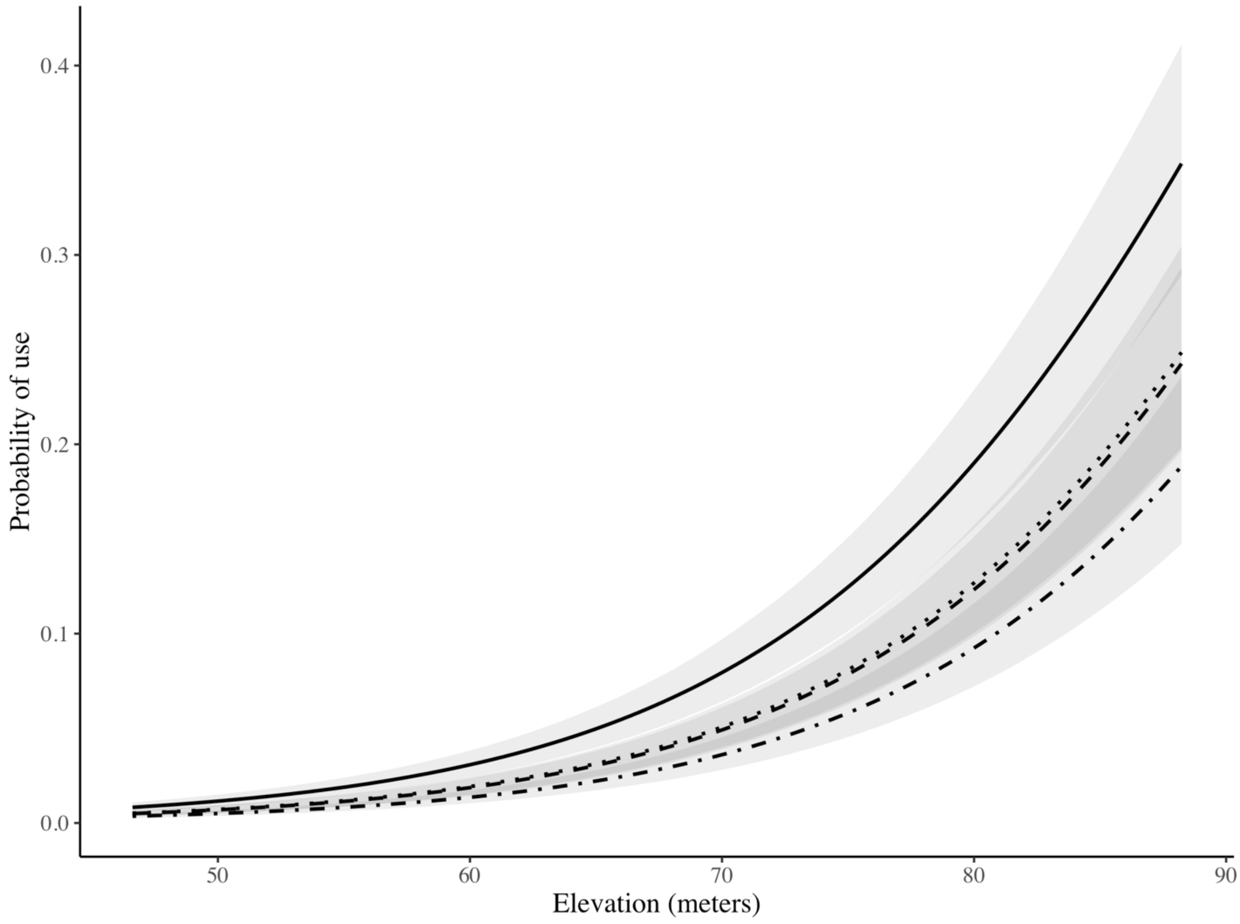

Figure 3.2: Probability (with 95% credible intervals) of gopher tortoise (*Gopherus polyphemus*) use as a function of elevation across each level of soil suitability (highly = solid line, moderately = dashed line, less = dotted line, and unsuitable = dot dashed line). Gopher tortoise telemetry data were collected in a private, working forest dominated by planted loblolly pine (*Pinus taeda*) located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018 – 2020.

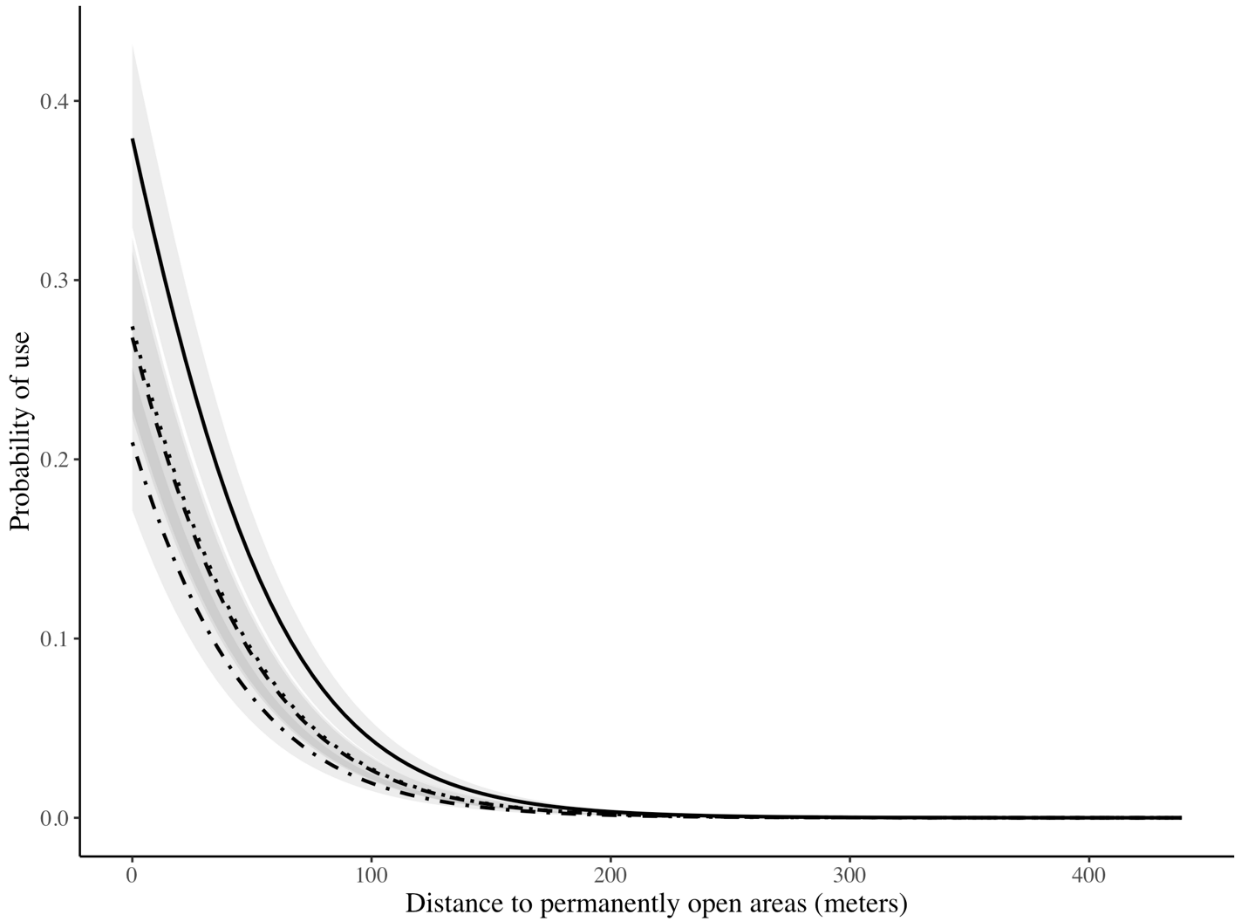

Figure 3.3: Probability (with 95% credible intervals) of gopher tortoise (*Gopherus polyphemus*) selection as a function of distance to permanently open areas across each level of soil suitability (highly = solid line, moderately = dashed line, less = dotted line, and unsuitable = dot dashed line). Gopher tortoise telemetry data were collected in a private, working forest dominated by planted loblolly pine (*Pinus taeda*) located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018 – 2020.

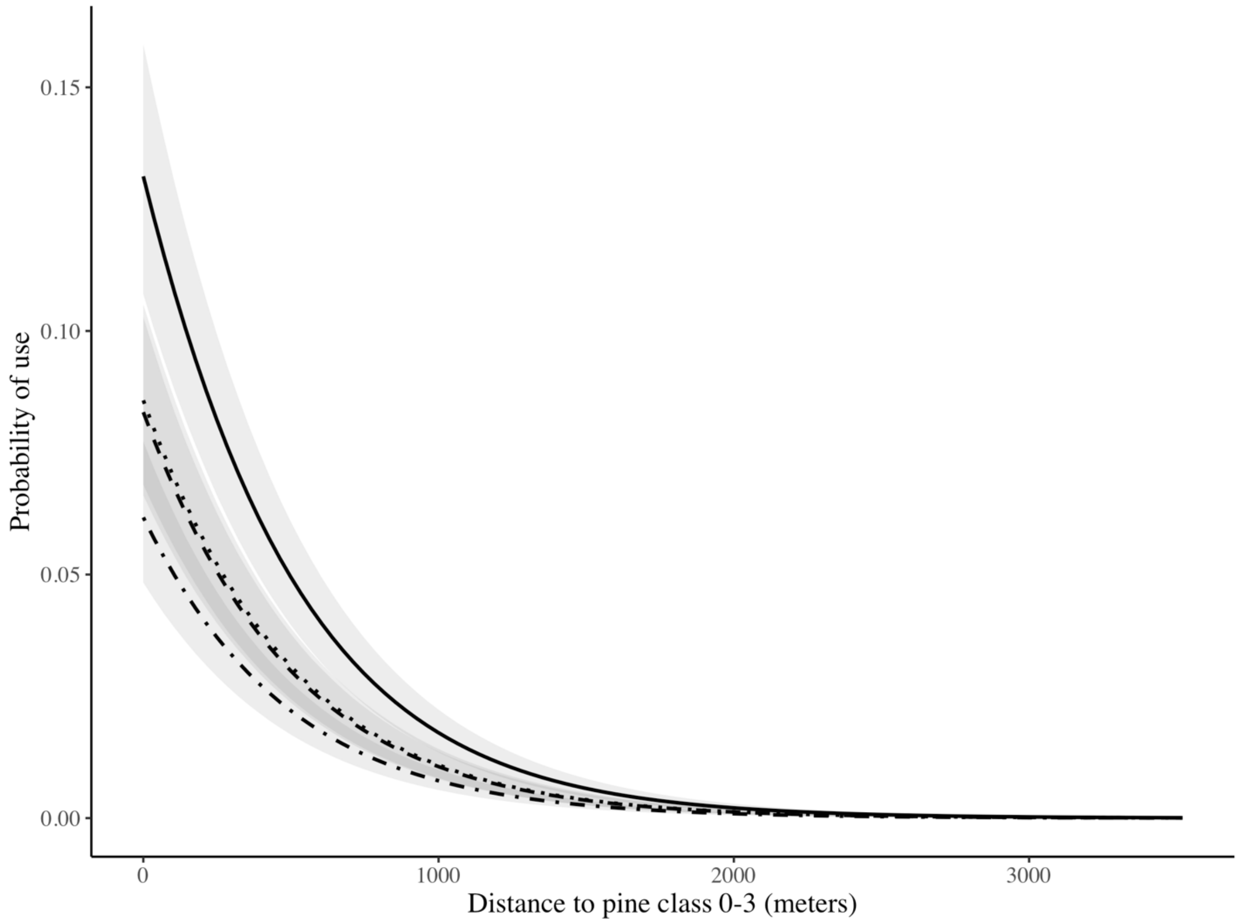

Figure 3.4: Probability (with 95% credible intervals) of gopher tortoise (*Gopherus polyphemus*) use as a function of distance to pine class 0-3 across each level of soil suitability (highly = solid line, moderately = dashed line, less = dotted line, and unsuitable = dot dashed line). Gopher tortoise telemetry data were collected in a private, working forest dominated by planted loblolly pine (*Pinus taeda*) located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018 – 2020.

CHAPTER 4

GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*) VERTEBRATE BURROW COMMENSALS WITHIN A PRIVATE, WORKING FOREST LANDSCAPE[3]

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[3] Marshall, C.D., J. A. Martin, A. L. Larsen-Gray, J. C. Maerz. To be submitted to *Journal of Wildlife Management*.

Abstract

The gopher tortoise (*Gopherus polyphemus*) is a keystone species endemic to the Coastal Plain ecoregion of southeastern United States. Gopher tortoises excavate extensive burrows that are used by over 60 vertebrate and 300 invertebrate species. Our understanding of burrow commensals has generally been limited to longleaf pine (*Pinus palustris*) savannah and xeric uplands and shrublands, excluding private, working pine (*Pinus* spp.) landscapes that are known to harbor tortoise populations. Therefore, we used passive infrared wildlife cameras to document vertebrate burrow commensals and evaluate differences in community composition across burrow classifications (i.e., abandoned, active, and inactive) within a private, working loblolly pine (*Pinus taeda*) landscape located in the Upper Coastal Plain ecoregion of Georgia, USA. The composition of the vertebrate commensal community documented in our study was similar to previous studies. However, we observed two undocumented bird species using burrow aprons, the red-headed woodpecker (*Melanerpes erythrocephalus*) and yellow-throated warbler (*Setophaga dominica*). Additionally, the vertebrate commensal community did not differ across tortoise burrow classifications in our study, indicating that burrows, regardless of classification, may provide a similar suite of resources (e.g., refugia, forage) to commensals inhabiting working, private loblolly pine landscapes. Our study contributes to prior evidence of the importance of gopher tortoise burrows as a resource for other wildlife and indicates that burrow protection, regardless of classification (e.g., abandoned), may positively effect commensal species conservation.

Key words: Gopher tortoise, *Gopherus polyphemus*, burrow commensals, burrow associates, private working forest landscape, *Pinus* spp., loblolly pine, *Pinus taeda*, Georgia

Introduction

The gopher tortoise (*Gopherus polyphemus*; hereafter, tortoise) is an ecosystem engineer and considered a keystone species within the southeastern Coastal Plain ecoregion of the United States (e.g., Young and Goff 1939, Lips 1991, Kinlaw and Grasmueck 2012, Catano and Stout 2015, Dziadzio and Smith 2016, Potash et al. 2020). Tortoises excavate extensive burrows whose construction and maintenance alter local abiotic and biotic characteristics (Kaczor and Hartnett 1990, Kinlaw and Grasmueck 2012, Dziadzio and Smith 2016). Burrow construction disturbs local soil conditions (e.g., organic matter concentrations, pH levels), providing appropriate conditions (e.g., bare soil) for pioneer plant species (Kaczor and Hartnett 1990). Tortoise burrows and burrow aprons also provide resources (e.g., refugia, forage, nesting sites) for more than 300 invertebrate and 60 vertebrate species (Young and Goff 1939, Witz et al. 1991, Lips 1992, Alexy 2003, Catano and Stout 2015, Dziadzio and Smith 2016, White and Tuberville 2017, Potash et al. 2020, Murphy et al. 2021). However, uncertainty exists regarding potential declines in tortoise populations and the affect that may have on the species that use tortoise burrows in some capacity (e.g., refugia, forage; Hermann et al. 2002, McCoy et al. 2006, Berish and Leone 2014, Catano and Stout 2015).

Tortoise burrow use by commensal species can be obligate or facultative with burrow use varying in frequency based on vegetation composition and structure, season, and burrow density and classification (Witz et al. 1991, Hyslop et al. 2009, Catano and Stout 2015, Dziadzio and Smith 2016, Potash et al. 2020). Only a few species, including the gopher frog (*Rana capito*), eastern indigo snake (*Drymarchon couperi*), and Florida mouse (*Podomys floridanus*), have been identified as species whose persistence relies primarily on presence of tortoise burrows (i.e., obligate commensals; Layne and Jackson 1994, Kent et al. 1997, Alexy et al. 2003, Hyslop et al.

2009, Roznik and Johnson 2009). However, our understanding of the relationships and dynamics between tortoise burrows and many of the other invertebrate and vertebrate commensals is currently limited. Furthermore, we have an incomplete understanding of the composition of invertebrate and vertebrate commensal communities across multiple landscapes inhabited by tortoises (e.g., longleaf pine [*Pinus palustris*] savannah, xeric shrubland, private, working pine [*Pinus* spp.] landscapes).

Private lands have received considerable attention regarding their capacity to support tortoise populations and aid in conservation strategies (Hermann et al. 2002, Underwood et al. 2012). Currently, private lands encompass > 80% of the species' range. However, these landscapes, especially private working lands, remain relatively understudied with regards to tortoise ecology (Hermann et al. 2002, Underwood et al. 2012, Greene et al. 2020). Private, working forest landscapes are common within the range of the tortoise and tortoises are known to inhabit and persist within these landscapes (Jones and Dorr 2004, Wigley et al. 2012, Duffie 2020). Studies of burrow commensals have generally been restricted to longleaf pine savannah and xeric shrublands within non-production pine landscapes (e.g., military installations; Witz et al. 1991, Alexy et al. 2003, Catano and Stout 2015, Dziadzio and Smith 2016, Potash et al. 2020, Murphy et al. 2021). No published information exists regarding invertebrate and vertebrate use of tortoise burrows within private, working forest landscapes.

Our objectives were to identify vertebrate burrow commensals within a private, working forest landscape and determine if the burrow commensal community differed in composition across burrow classifications (i.e., abandoned, active, and inactive). We expected to observe a similar suite of species using tortoise burrows as those identified in previous commensal studies, with minor differences in species observed resulting from differences in sampling timeframe (e.g., summer, fall), location (e.g., within the range of certain commensal species) or presence of specific landscape features (e.g., ephemeral wetlands) required by specific commensal species. Furthermore, we hypothesized that the composition of the burrow commensal community would differ across burrow classifications. We predicted that each burrow classification would support a unique composition of commensal species as suggested by previous commensal studies, with active and abandoned burrows supporting distinct communities and inactive burrows supporting a transitional community between active and abandoned burrow commensals (Lips 1991, Dziadzio and Smith 2016).

Study Area

Our study was conducted in a private, working forest landscape located in the Upper Coastal Plain ecoregion of Georgia, USA. The site was 32.44 km^2 and consisted predominately of managed loblolly pine planted in even-aged stands (22.91 km^2), with adjacent stands differing in edaphic (e.g., elevation, soil characteristics) and vegetation conditions (e.g., herbaceous understory, canopy cover) because of the timing of forest management (e.g., stand establishment, mid-rotational thinning, final harvest). Managed pine stands were interspersed with streamside management zones and hardwood areas (5.49 km^2), roads (paved and unpaved; 0.78 km^2), non-forest areas (e.g., wildlife openings, food plots; 0.09 km^2), and utility rights-of-way (0.39 km^2). Lands surrounding our study area consisted of agricultural fields, loblolly pine stands, suburban and rural development, and pine stands not managed primarily for timber production. The climate was subtropical with a mean annual temperature of 18.5° C and mean annual precipitation of 130 cm (National Oceanic and Atmospheric Administration 2021).

Methods

We used passive infrared wildlife cameras (Spartan SR1-BK, Duluth, GA, USA) to identify vertebrate commensals using tortoise burrows from June – August in 2018 and 2019. Burrows used in our study were derived from datasets of burrow detections from other studies conducted on the study site during 2018 and 2019 (Marshall, University of Georgia, unpublished data). Within these datasets, we classified burrows as active (half-moon shaped opening and entrance often having plastron skid marks or footprints), inactive (minimal sign of recent use), or abandoned (burrow opening collapsed or shape was altered; Stober and Smith 2010, Wigley et al. 2012). We only monitored adult gopher tortoise burrows (burrow width ≥ 15cm; Alford 1980, Doonan and Stout 1994). We monitored all burrows for 14 days (a single set), with 3 sets occurring in 2018 and 4 sets in 2019. Within each set, we evenly split 18 cameras across abandoned, active, and inactive tortoise burrows (6 cameras per category). We visually inspected all photos and identified detected vertebrates to species. However, we combined all detections of *Peromyscus* spp. into a single group due to difficulty in accurately identifying species. We only included observations of individuals using tortoise burrows or burrow aprons in some manner (e.g., entering or leaving the burrow). We recorded date, time, a unique burrow identification, and burrow status (i.e., active, inactive, or abandoned) for each detected individual. We considered multiple detections of the same species within 10 minutes of each other to be a single detection event. We conducted all research under the University of Georgia Institutional Animal Care and Use Committee (IACUC) protocol A2018 01-018-Y3-A0.

Statistical Analyses

We used rarefaction implemented in the vegan package in R to identify if species richness differed across sampling years because of unequal sampling effort (Oksanen et al. 2020, R Core Team 2020). We also used linear regression in R to determine if unequal sampling across years resulted in differences in the number of observations. We used non-metric multidimensional scaling to investigate dissimilarity in vertebrate commensal community composition across burrow classifications. Non-metric multidimensional scaling was implemented using the vegan package in R (Oksanen et al. 2020, R Core Team 2020). We used a Bray-Curtis distance measure as this is a commonly used distance measure when conducting ordinations with ecological data as it is invariant to changes in units and has the capacity to deal data sets containing multiple zeros (e.g., count data; Rees et al. 2004). We visually inspected Shepard plots and stress values (e.g., stress ≤ 0.05 provides an excellent representation of the data, stress > 0.2 provides a poor representation of the underlying data) to determine if the data was being adequately represented within a certain number of dimensions (e.g., two or three dimensions; Clark 1993). We then used the function "adonis" within the vegan package in R to test the significance of the environmental variables (i.e., burrow classification) using permutation tests (Oksanen et al. 2020, R Core Team 2020). We considered all tests significant at $\alpha = 0.05$.

Results

We had 698 detections encompassing 30 vertebrate species across 1764 trap days and 125 tortoise burrows (Figure 4.1). One burrow was removed from the dataset due to a malfunctioning camera. Sampling effort varied across years, with 756 sampling days in 2018 and 1008 sampling days in 2019. We found no indication of differences in species richness or total observations (z =

-0.46, p-value = 0.63) because of unequal sampling across survey years (Figure 4.2). We detected 9 reptile, 1 amphibian, 12 bird, and 8 mammal species using tortoise burrows or burrow aprons (Tables 4.1 – 4.3). We were unable to determine the species of 8 snake and 6 bird observations. However, we identified the bird observations to order Passeriformes. Non-metric multidimensional scaling attained a convergent 3-dimensional solution with a stress value of 0.15. This stress value indicates that the underlying data is well represented in 3 dimensions. We could have continued to reduce the stress value by increasing the number of dimensions (e.g., 5-dimensional). However, increasing the dimensionality beyond 3 would significantly reduce our ability to interpret model results. The composition of vertebrate burrow commensal community did not differ across abandoned, active, or inactive burrows (r^2 = 0.1, p-value = 0.48; Figure 4.3). We conducted a *post-hoc* ordination to determine if mammal species composition differed across burrow classifications based on unique patterns emerging after visual inspection of the data (Figure 4.1). We found no difference in mammal species composition across abandoned, active, and inactive burrows (r^2 = 0.14, p-value = 0.16).

Discussion

We documented a diverse assemblage of vertebrate species associated within private, working pine forests using abandoned, active, and inactive gopher tortoise burrows. The commensal community observed in our study was similar in composition to those described in previous studies conducted in non-private, working forests, such as military installations, longleaf pine forests, and xeric uplands and shrublands (e.g., Lips 1991, Dziadzio and Smith 2016, White and Tuberville 2017, Murphy et al. 2021). A lack of observations of certain commensal species, specifically amphibian and reptile species, within our study site may be a result of landscape characteristics, seasonality, or the survey method (e.g., camera trapping) employed. For example, we did not observe gopher frogs, a known obligate commensal, using tortoise burrows even though our site was located within the species' range (Kent et al. 1997, Dziadzio and Smith 2016). Furthermore, our study was conducted during summer (May – August) and, thus, may explain why some commensal species were not detected or not detected in greater numbers. Certain commensal species increase use of tortoise burrows during different seasons, such as eastern indigo snakes increasing use during the winter (Lips 1991, Hyslop et al. 2009). Sampling across multiple seasons within our study site may increase the number of commensal species observed and provide insight into how commensal use of tortoise burrows shifts in response to season (Lips 1991). Furthermore, using passive infrared cameras may have biased our observations towards larger species, as movements of smaller reptiles and amphibians (e.g., six-lined racerunner [*Aspidoscelis sexlineata*], eastern spadefoot toad [*Scaphiopus holbrookii*]) may not have reliably triggered the cameras (Amber et al. 2021). Furthermore, ectotherms and small mammals, such as shrews, voles, and mice, can have surface temperatures that are similar to background surfaces (e.g., plants, bare ground), resulting in the infrared sensor not detecting an individual (Glen et al. 2013, Amber et al. 2021).

Contrary to our initial prediction, we did not observe a unique commensal community associated with each of the three burrow classifications. We documented a similar vertebrate commensal community using abandoned, active, and inactive tortoise burrows. Our results suggest that tortoise burrows, regardless of classification, may provide a similar suite of resources (e.g., forage, refugia) to vertebrate commensals inhabiting our study site. Previous studies have documented differences in the frequency of burrow use by taxa (e.g., mammal, reptile) and species (e.g., gopher frog) among burrow classifications (Lipps 1991, Witz et al.

1991, Kent et al. 1997, Dziadzio and Smith 2016). It has been suggested that differences in commensal burrow use arise from active burrows providing additional resources to commensal species, such as recently deposited tortoise feces, compared to abandoned and inactive burrows (Lipps 1991, Dziadzio and Smith 2016). However, documented differences in commensal composition may relate more to the spatial distribution of surveyed tortoise burrows than burrow classification (Kent et al. 1997). In other words, surveyed active burrows may have been clumped within areas exhibiting specific vegetation characteristics or adjacent to important landscape features (e.g., ephemeral wetlands) that are well-suited or required for specific taxa or species (Witz et al. 1991). Although we did not observe an effect of burrow classification on commensal mammal community composition, we did observe unique patterns of burrow use by meso-mammals. Meso-mammals, such as the nine-banded armadillo (*Dasypus novemcinctus*) and Virginia opossum (*Didelphis virginiana*), were detected more often using abandoned and inactive burrows than active burrows (Figure 4.2). It is likely that meso-mammals prefer abandoned and inactive burrows as they are less likely to be occupied by a tortoise, potentially reducing competition for space within the burrow and enabling the species, specifically nine-banded armadillos, to permanently modify the existing structure (e.g., widening the burrow entrance). It is also possible that meso-mammals evict tortoises from burrows although this behavior has yet to be observed and documented.

We observed two previously undocumented bird species, the red-headed woodpecker (*Melanerpes erythrocephalus*) and yellow-throated warbler (*Setophaga dominica*), using tortoise burrow aprons. Based on the foraging habits (e.g., occasional ground forager) of the red-headed woodpecker, it is possible that the detected individual was foraging for invertebrates associated with burrows or the burrow aprons (Williams 1975). It is plausible that the observed yellow-throated warbler was using the burrow apron for reasons other than foraging (e.g., dust bathing), as the species is a foliage and bark gleaner of the upper forest canopy (Morse 1974, Gabbe et al. 2002). However, we only had a single observation of each species. These observations do not provide a strong indication of behavior (e.g., foraging, dust bathing), making it difficult conclude how these species may use tortoise burrows or burrow aprons. It is also possible that observations of these species were coincidental and not related to their use of tortoise burrows or burrow aprons.

Our study demonstrates the importance of tortoise burrows in providing resources (e.g., refugia, forage) for a range of wildlife species associated with private, working forest landscapes. Therefore, protecting tortoise burrows within these landscapes may positively affect commensal wildlife, including species of conservation concern, such as the Florida pine snake (*Pituophis melanoleucus*). Moreover, our results show that commensal species used inactive and abandoned tortoise burrows similar to active tortoise burrows. Therefore, protecting inactive and abandoned burrows may be of conservation benefit on private, working forest landscapes for some wildlife species. We encourage continued monitoring of tortoise burrow commensal communities to better understand how burrows contribute to species abundance and persistence within these landscapes. For future research, we recommend using video recordings to monitor vertebrate commensals over photos when possible (Dziadzio and Smith 2016, White and Tuberville 2017). Video recordings would enable researchers to observe commensal behaviors and determine the how and why commensal species may use burrows. Lastly, we recommend greater attention to measuring invertebrate commensal use of tortoise burrows.

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Tables and Figures

Table 4.1: Number of unique observations of bird species using gopher tortoise (*Gopherus polyphemus*) burrows or burrow aprons. Data were collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) stands located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018 – 2019.

Species	Detections
Bachman's sparrow (*Peucaea aestivalis*)	11
Brown thrasher (*Toxostoma rufum*)	34
Carolina wren (*Thryothorus ludoviicianus*)	135
Eastern bluebird (*Sialia sialis*)	3
Eastern towhee (*Pipilo erythrophthalmus*)	26
Field sparrow (*Spizella pusilla*)	3
Gray catbird (*Dumetella carolinensis*)	15
Indigo bunting (*Passerina cyanea*)	4
Northern cardinal (*Cardinalis cardinalis*)	2
Northern mockingbird (*Mimus polyglottos*)	6
Passerine spp.	6
Red-headed woodpecker (*Melanerpes erythrocephalus*)	1
Yellow-throated warbler (*Setophaga dominica*)	1
Total	247

Table 4.2: Number of unique observations of herptile species using gopher tortoise (*Gopherus polyphemus*) burrows or burrow aprons. Data were collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) stands located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018 – 2019.

Species	Detections
Black racer (*Coluber constrictor*)	4
Broadheaded skink (*Eumeces laticeps*)	1
Coachwhip (*Masticophis flagellum*)	4
Eastern diamondback rattlesnake (*Crotalus adamanteus*)	5
Eastern box turtle (*Terrapene carolina*)	3
Eastern kingsnake (*Lampropeltis getula*)	1
Five-lined skink (*Eumeces fasciatus*)	3
Pine snake (*Pituophis melanoleucus*)	5
Six-lined racerunner (*Cnemidophorus sexlineatus*)	13
Snake spp.	8
Bufo (*Anaxyrus*) spp.	11
Total	58

Table 4.3: Number of unique observations of mammal species using gopher tortoise (*Gopherus polyphemus*) burrows or burrow aprons. Data were collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) stands located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018 – 2019.

Species	Detections
Cotton rat (*Sigmodon hispidus*)	19
Eastern cottontail (*Sylvilagus floridanus*)	83
Fox squirrel (*Sciurus niger*)	12
Nine-banded armadillo (*Dasypus novemcinctus*)	100
Peromyscus spp.	112
Pine vole (*Microtus pinetorum*)	1
Raccoon (*Procyon lotor*)	9
Virginia opossum (*Didelphis virginiana*)	57
Total	393

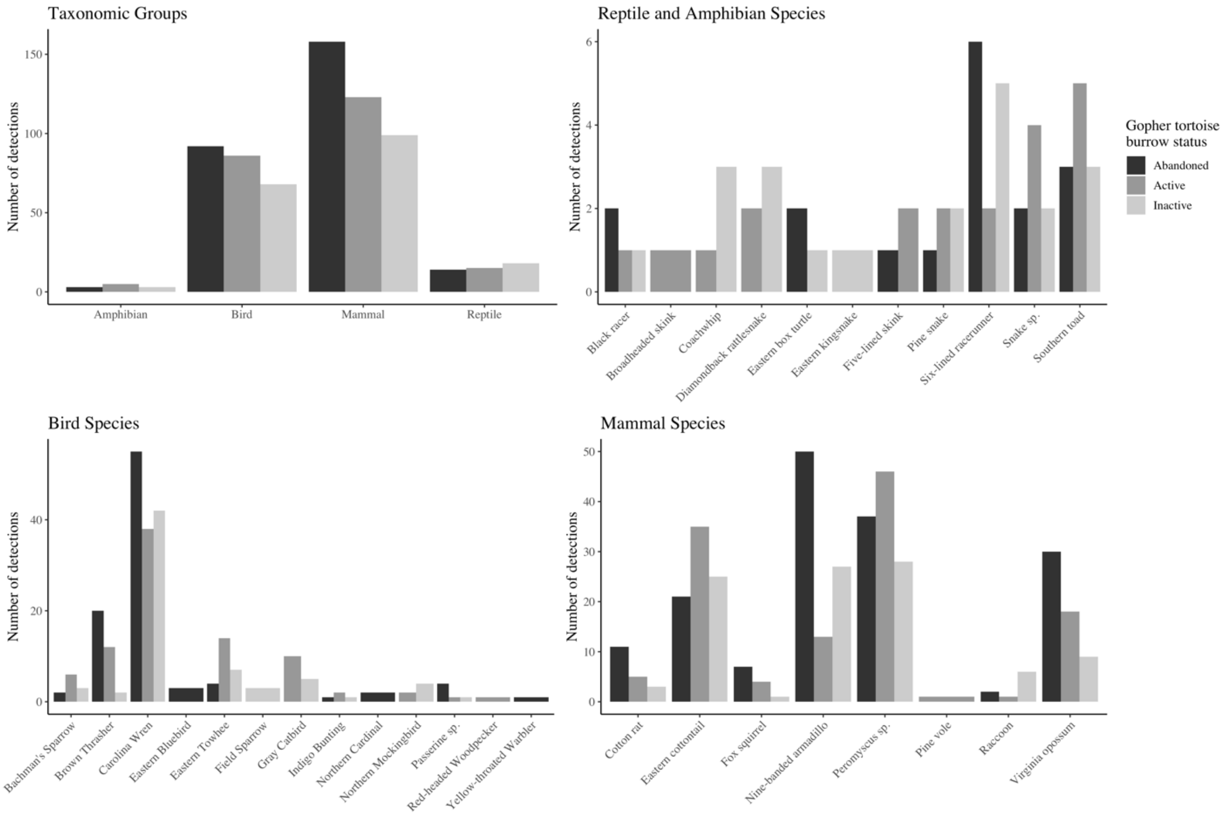

Figure 4.1: Number of unique observations of vertebrate burrow commensals by taxonomic group (top left), reptile and amphibian species (top right), bird species (bottom left), and mammal species (bottom right). Vertebrate burrow commensal data were collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) stands located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018 – 2019.

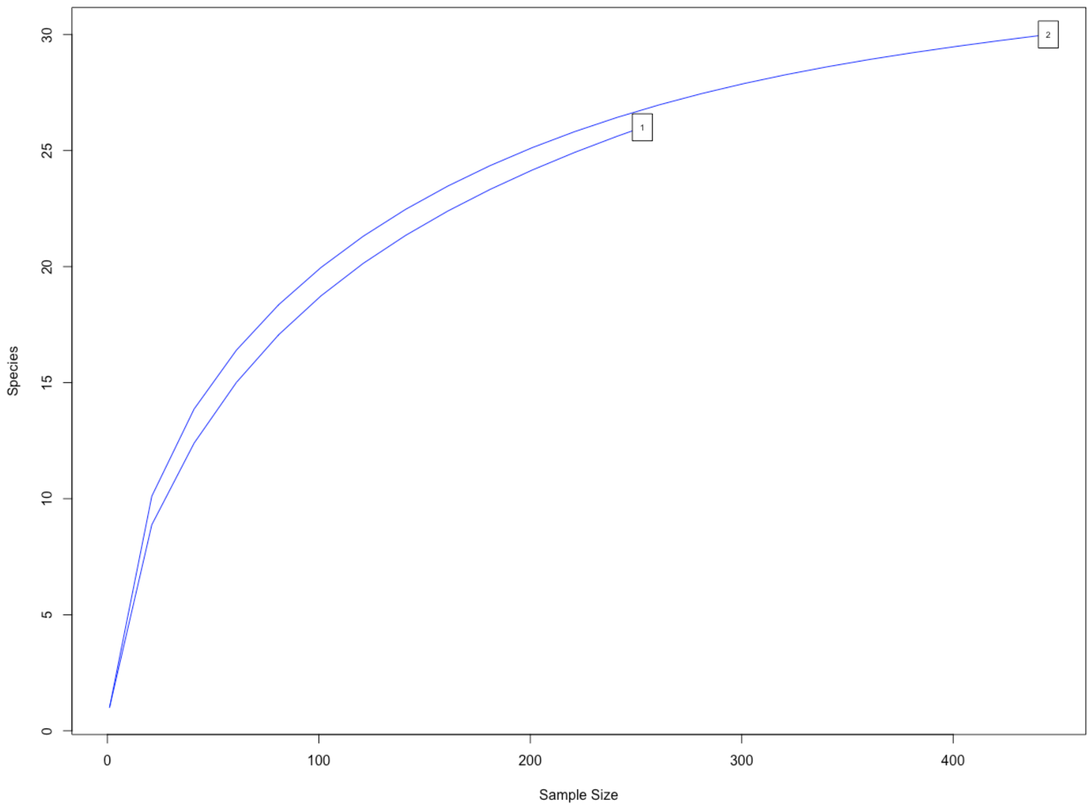

Figure 4.2: Rarefaction curves of species richness during 2018 (1) and 2019 (2). Vertebrate burrow commensal data were collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) stands located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018 – 2019.

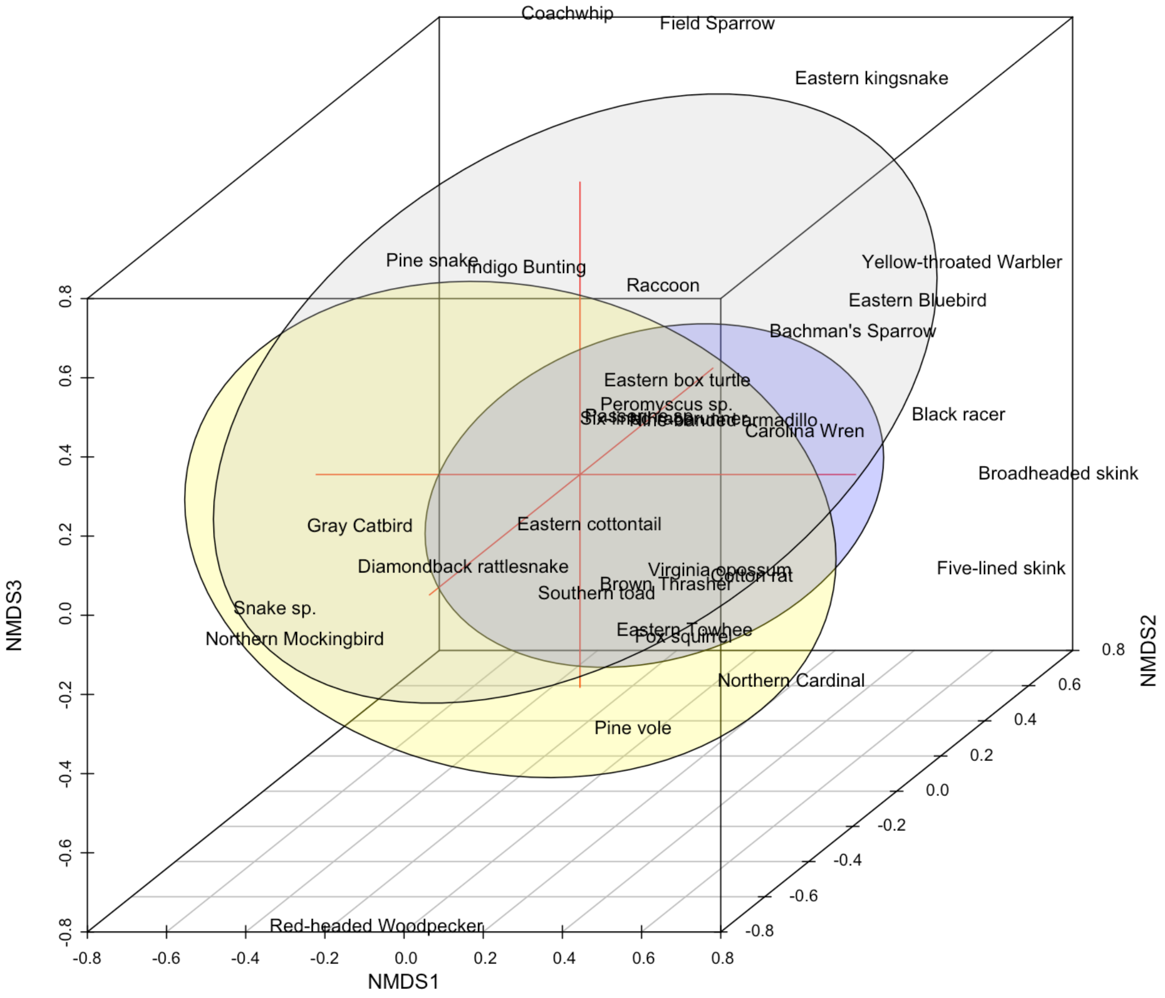

Figure 4.3: Three axes of non-metric multidimensional scaling of the vertebrate commensal community across abandoned (blue), active (yellow), and inactive (gray) gopher tortoise (*Gopherus polyphemus*) burrows. Vertebrate burrow commensal data were collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) stands located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018 – 2019.

CHAPTER 5

CONCLUSIONS

The gopher tortoise (*Gopherus polyphemus*; hereafter, tortoise) is an ecologically important species endemic to the Coastal Plain ecoregion of the southeastern United States (e.g., Young and Goff 1939, Lips 1991, Kinlaw and Grasmueck 2012, Dziadzio and Smith 2016, Potash et al. 2020). Tortoise populations have historically experienced population declines, with these declines attributed to habitat loss (e.g., conversion to agriculture and agroforestry), fragmentation, and degradation (e.g., suppression of natural disturbance regimes), disease, and human exploitation (e.g., Hermann et al. 2002, McCoy et al. 2006, Berish and Leone 2014). This has resulted in tortoise populations west of the Mobile and Tombigbee Rivers in Alabama, Mississippi, and Louisiana, USA being listed as threatened under the federal Endangered Species Act (U.S. Fish and Wildlife Service 1987). Tortoise populations east of these river systems in Alabama, Florida, Georgia, and South Carolina, USA were designated as a candidate species (U.S. Fish and Wildlife Service 2011). Uncertainty regarding population status and a recent proposal to reevaluate the species' designation by the U.S. Fish and Wildlife Service has stimulated research aimed at identifying population demographics and viability, movement patterns, and habitat associations throughout the species' range (e.g., Greene et al. 2019, Duffie 2020, Greene et al. 2020, Folt et al. 2021).

Private lands encompass a large portion of the tortoises' range and are predicted to become an increasingly important component of tortoise conservation (Hermann et al. 2002, Underwood et al. 2012). Private, working forest landscapes that primarily consist of even-aged pine (*Pinus* spp.) stands planted to produce merchantable forest products (e.g., timber, pulp wood, utility poles) are included in this designation. Private, working forests are common across the species' range and tortoise populations are well documented within these landscapes (Aresco and Guyer 1999, Jones and Dorr 2004, Diemer Berish et al. 2012, Wigley et al. 2012, Duffie 2020, Greene et al. 2020). However, tortoise ecology within these landscapes is relatively understudied, particularly in private, working forest landscapes under more contemporary management practices (e.g., Jones and Dorr, Wigley et al. 2012, Duffie 2020). Therefore, the major objectives of my study were to provide novel information and to build on previous research regarding tortoise use and habitat associations within these landscapes.

Herein I identified permanently open areas, such as forest roads and utility rights-of-way, and forest stands characterized by early successional vegetation (e.g., pine 0-3 years) as important areas to tortoises within a private, working forest landscape. Results from my study support the hypothesis that permanently open areas and forest stands characterized by early successional vegetation are attractive to tortoises because of the open canopy conditions that allow for the growth of perennial herbaceous forage (Wigley et al. 2012, Rautsaw et al. 2018, Duffie 2020, Greene et al. 2020). Although I documented greater densities of active burrows and selection for areas proximate to permanently open areas and forest stands characterized by early successional vegetation, it remains unclear if and how these areas interact to enable tortoise populations to persist within these landscapes. Although adult tortoises were persisting within my study area by using permanently open areas and forest stands characterized by early successional vegetation, it is unclear if these areas provide adequate nesting sites or resources required by hatchling and juvenile tortoises. In other words, it is unclear if these areas provide sufficient resources (e.g., nest sites, cover for hatchlings) to facilitate recruitment. Future studies should focus on estimating demographic parameters and resource selection across tortoise age classes to improve our understanding of how permanently open areas and stand conditions influence tortoise use and population dynamics within private, working forest landscapes. Results from these studies will provide much needed information that can be used to generate management recommendations aimed at tortoise conservation within these landscapes.

I developed a spatially explicit distance sampling model that was used to estimate abandoned and active tortoise burrow density and evaluate relationships between burrow density and edaphic and vegetative structural conditions within a private, working forest landscape. I was able to evaluate covariates, such as distance to forest roads, that have otherwise proved difficult to quantify using standard distance sampling approaches (e.g., Mizel et al. 2018, Duffie 2020). Results from my study indicate that forest roads and forest stands characterized by early successional vegetation may interact to support tortoise populations within the surveyed private, working forest landscape. Based on our results, tortoise burrow surveys should not exclude non-pine stand related areas, such as forest roads and utility rights-of-way. Sampling designs should encapsulate all components (e.g., early rotational stands, mature stands, forest roads, utility rights-of-way) of private, working forest landscapes as this will improve our understanding of tortoise habitat associations and better inform management practices aimed at increasing the compatibility of these forests with tortoise conservation. Furthermore, forest and wildlife managers should shift their focus from attaining a minimum viable population to identifying the parameters that are important to tortoise population stability within private, working forest landscapes.

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SUPPLEMENTARY MATERIALS A

I implemented two different transect survey designs across the 2018 and 2019 survey years. My objective for both survey designs was to evaluate associations between tortoise burrow density and forest stand conditions (e.g., vegetation density, edaphic factors). Therefore, transects were restricted to forest stands and did not extend into non-commercial pine areas (e.g., utility rights-of-way, streamside management zone) present within our study site. The 2018 survey design consisted of 214 transects, with 118, 500m transects placed within the interiors of randomly selected forest stands (hereafter; stand interior transects). The remaining 96 transects were 200m in length and placed parallel of forest roads and adjacent to stands with interior transects when available (hereafter; road transects). The 2018 survey was specifically designed for use with standard distance sampling statistical approaches that use plot-level covariates (i.e., canopy cover averaged over an entire transect) compared to the 2019 survey that was designed for use with a spatially explicit distance sampling model (see Chapter 3). Results the 2018 survey were inconsistent with the 2019 results and contradicted the results of previous studies evaluating tortoise habitat associations (e.g., Jones and Dorr 2004, Wigley et al. 2012, Kowal et al. 2014, Duffie 2020). Differences in results across survey designs may be attributed to total area surveyed or to the total number of tortoise burrows detected. However, the survey designs covered a similar area (2.87km^2 vs. 2.23km^2) within my study site and I detected a similar number of burrows (117 vs. 112) across years. It is unclear as to what is causing the discrepancy between surveys. For transparency we have included the 2018 survey results for abandoned and active tortoise burrow density (Figure 6.1).

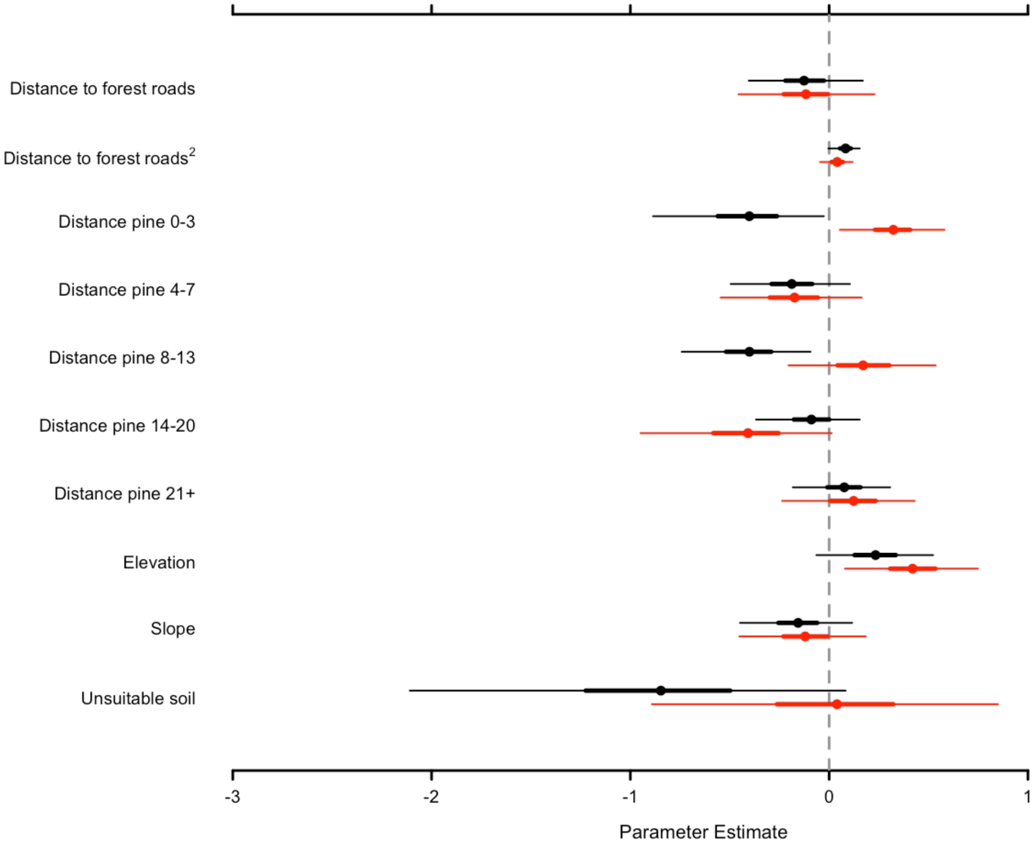

Figure A.1: Plot of posterior means (points) and 50% (thick lines) and 95% (thin lines) credible intervals for covariates included in a spatially explicit distance sampling model used to estimate densities of abandoned (black) and active (red) gopher tortoise (*Gopherus polyphemus*) burrows. Estimates were derived from line transect distance sampling data collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA in 2018.

SUPPLEMENTARY MATERIALS B

Table B.1: Mean and standard deviation of gopher tortoise (*Gopherus polyphemus*) weight (kg) and carapace length (cm) by sex. Data was collected from radio tagged tortoises captured in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA in 2018 and 2019.

Sex	Carapace length (cm)	Weight (kg)
Female	31.60 ± 1.89	5.52 ± 0.77
Male	30.37 ± 2.13	5.25 ± 0.79

Table B.2: Summary statistics of gopher tortoise (*Gopherus polyphemus*) home range size (ha) by sex. Data were collected from radio tagged tortoises captured in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018-2020.

Sex	N	Mean	Min	Max	Standard deviation	Standard error
Female	21	1.113	0.008	4.860	1.499	0.327
Male	34	5.115	0.136	46.230	8.978	1.540

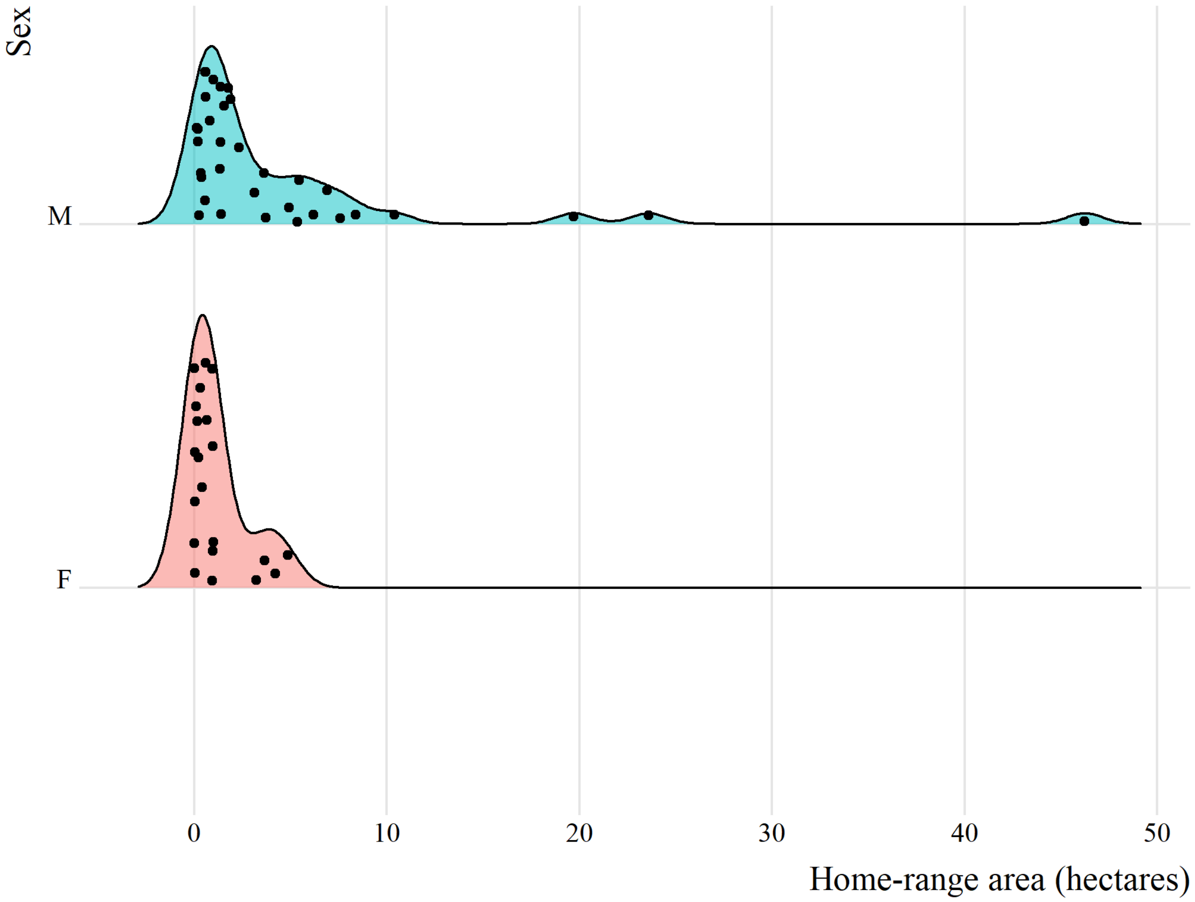

Figure B.1: Density distributions of gopher tortoise (*Gopherus polyphemus*) home range size (ha) by sex (F = female, M = male). Data were collected from radio tagged tortoises captured in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018-2020.

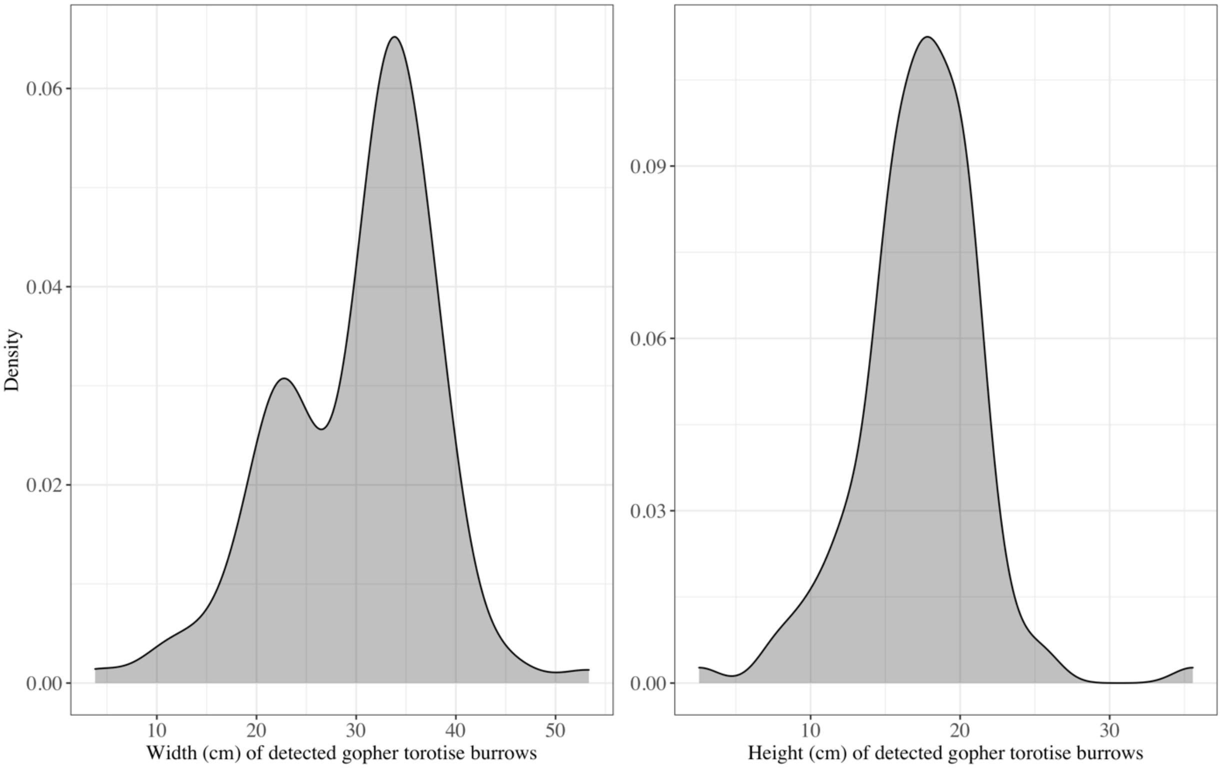

Figure B.2: Density distributions of gopher tortoise (*Gopherus polyphemus*) burrow widths (cm) and heights (cm). Data were collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA in 2019.

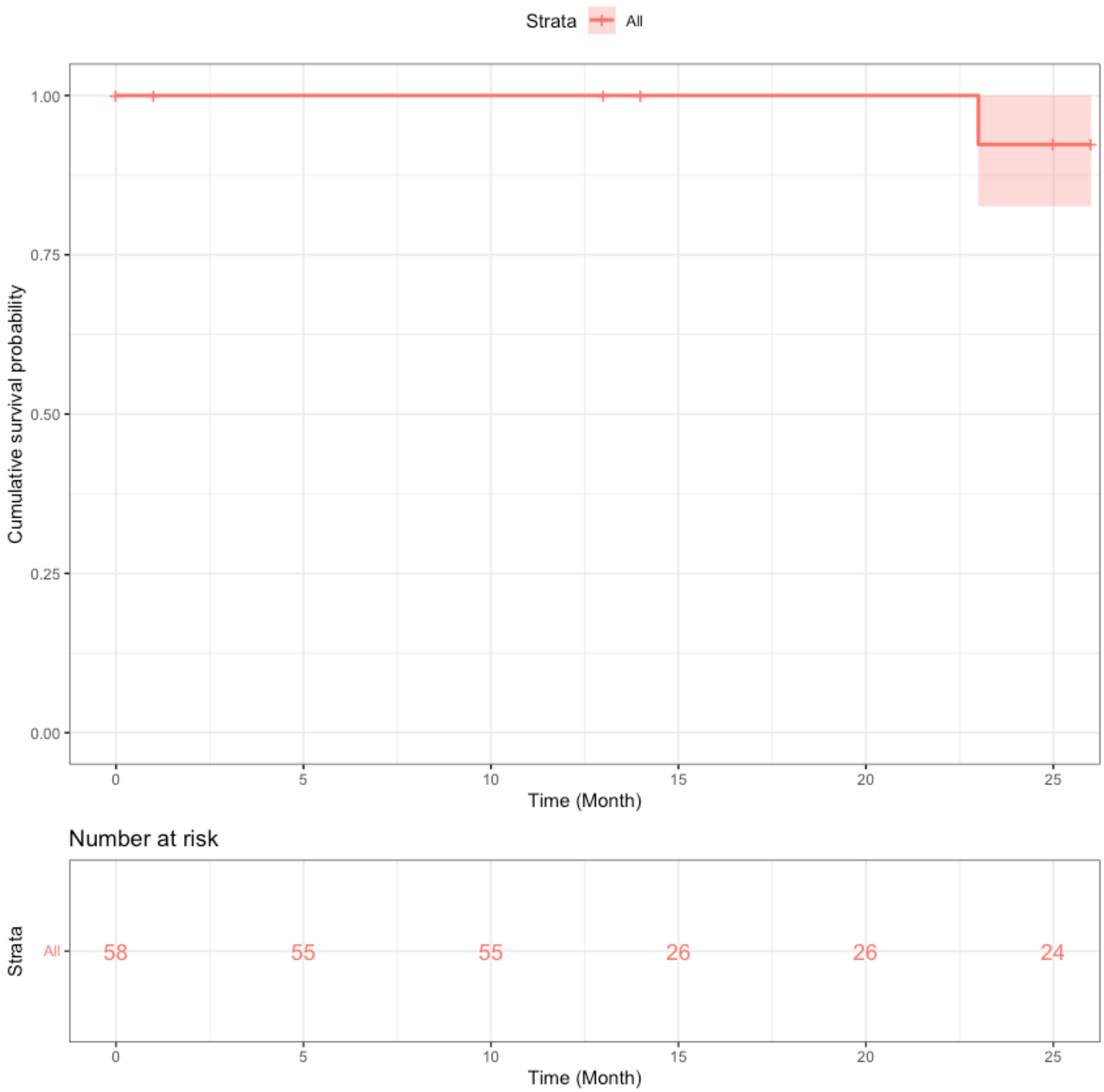

Figure B.3: Monthly survival of 58 radio-tagged adult gopher tortoises (*Gopherus polyphemus*). Data were collected in a private, working forest landscape dominated by planted loblolly pine (*Pinus taeda*) and located in the Upper Coastal Plain ecoregion of Georgia, USA from 2018-2020.